Phylogenetic relationships of the comb-footed spider subfamily Spintharinae (Araneae, Araneoidea, Theridiidae), with generic diagnoses and a key to the genera

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Abstract

The monophyly of Spintharinae is supported in agreement with previous analysis of Theridiidae by Agnarsson and Arnedo *et al*. We study the relationships of the genera within Spintharinae. Fourteen species in the genera *Chrosiothes*, *Episinus*, *Spintharus*, *Stemmops*, and *Thwaitesia* constituted the ingroup, while five species from the genera *Euryopis* and *Dipoena* (Hadrotarsinae), as well as *Latrodectus* and *Steatoda* (Latrodectinae), served as outgroup taxa. The character matrix included 49 morphological characters. Parsimony analyses using several character weighting strategies supported the monophyly of Spintharinae with *Stemmops* as sister to a clade that includes the remaining ingroup taxa. *Chrosiothes* emerged as sister to *Episinus* + *Spintharus* + *Thwaitesia* which formed a polytomy. The equally weighted, successive weighted, and preferred implied weight topologies, were all logically consistent. A key to the genera of Spintharinae and diagnoses for each genus are given.

Key words: Cobweb spiders, *Chrosiothes*, *Episinus*, *Spintharus*, *Stemmops*, *Thwaitesia,* key, diagnosis

Introduction

The Theridiidae, popularly known as cobweb or comb-footed spiders, ranks as one of the most species rich spider families, with 121 genera and 2,351 species distributed worldwide (Arnedo *et al*. 2004; Agnarsson 2004; Platnick 2013). Theridiids exhibit extreme diversity in morphology, ecology, and behavior, and show a particularly diverse array of web types, from simple to complex (Arnedo *et al*. 2004; Agnarsson 2004; Eberhard *et al*. 2008). Despite important recent advances in the systematics and classification of the family (e.g., Arnedo *et al*. 2004; Agnarsson 2004), generic relationships are not completely understood, and some theridiid genera are poorly delimited and probably para- or polyphyletic (Arnedo *et al*. 2004).

Theridiids are generalists feeding on whatever prey are caught in their webs; however, some are specialists, such as *Chrosiothes tonala* (Levi 1954), a predator of termites (Eberhard 1991). Most genera of the subfamily Spintharinae present a modified web. The genera *Spintharus*, *Episinus* and *Thwaitesia* build a web with an "H"-like shape, while *Chrosiothes* builds a sheet-like web, presumably because of a specialization for their prey (Eberhard 1991; Agnarsson 2004; Eberhard *et al*. 2008). Although all genera present sexual dimorphism in size, behavior differs considerably among genera. Also, the silken egg sacs are complex and diverse (Eberhard *et al*. 2008), with the outermost fibers densely spun in *Latrodectus*, while the outermost fibers are loosely woven in *Episinus* and *Thwaitesia* (Agnarsson 2004).

Levi and Levi (1962) made the first comprehensive effort to define the genera of the family Theridiidae. They reduced the number of genera from 140 to 50 and provided a classification. However, they did not address a formal higher classification or phylogeny. It was not until the work by Forster *et al*. (1990) that a formal proposal was made for two Theridiidae subfamilies, Hadrotarsinae and Spintharinae, with possible defining synapomorphies.

Yoshida (2001a, 2001b) further recognized four subfamilies: Hadrotarsinae, Episininae, Argyrodinae, and Theridiinae (the latter including Spintharinae and Monetinae).

More recently, Arnedo *et al.* (2004) proposed a phylogeny of Theridiidae based on nuclear and mitochondrial DNA characters. In their analysis, Spintharinae was considered sister to Hadrotarsinae, and both were sister to Argyrodinae. In turn, this clade was sister to *Anelosimus* plus Theridiinae (lost colular setae clade). Latrodectinae was sister to all other theridiids (Arnedo *et al.* 2004, fig. 3). They included the genera *Chrosiothes*, *Episinus*, *Spintharus*, *Stemmops*, and *Thwaitesia* of Spintharinae. Around the same time, Agnarsson (2004) performed a comprehensive analysis of the relationships of theridiid genera based on morphological characters (Fig. 1). Taxonomic sampling was quite dense, as well as the ample exploration and selection of morphological characters. Spintharinae, in that study, was sister to a large clade composed of Pholcommatinae, Argyrodinae, and Theridiinae, plus *Anelosimus* and *Kochiura*, wich lacked subfamily membership.

Agnarsson's (2004) work provides a solid hypothesis of phylogenetic relationships within Theridiidae on the basis of morphology. His analysis incorporated 53 theridiid taxa in 32 genera scored for 242 morphological characters. Nonetheless, certain phylogenetic questions still require attention. One concerns the phylogenetic relationships within the subfamily Spintharinae, for which not all genera were included. The monophyly of this subfamily, as proposed by Agnarsson (2004), with the genera *Episinus*, *Spintharus*, *Thwaitesia*, *Stemmops*, *Moneta*, and *Chrosiothes*, also requires further testing. In his phylogenetic hypothesis, Agnarsson included *Episinus*, *Spintharus,* and *Thwaitesia*, supported by several synapomorphies. Nonetheless, *Stemmops* emerged as a member of Pholcommatinae. Herein, we further evaluate *Stemmops*' position by including three species in addition to the one in Agnarsson's study.

We attempt to further test the monophyly of Spintharinae based on morphological characters, with the inclusion of *Chrosiothes* and a reevaluation of *Stemmops*' position (with *Moneta* as the only genus of the subfamily missing); test the monophyly of *Stemmops*, *Episinus*, *Thwaitesia*, and *Chrosiothes*, all of which had two or more species in the analysis, to try to better understand the generic relationships within Spintharinae. This work also includes a modified diagnosis for each of the Spintharinae genera, as well as a key to the genera of the subfamily.

Material and methods

Taxon sampling. Agnarsson's (2004) recognized the subfamilies, Hadrotarsinae, Latrodectinae, Spintharinae, Pholcommatinae, Argyrodinae, and Theridiinae, and their relationships are taken as the current reference phylogeny. According to Agnarsson (2004), Hadrotarsinae is sister to all other theridiids (but see Arnedo *et al.* 2004), and within the latter group, Latrodectinae is sister to the remaining theridiids, which includes Spintharinae as the most basal member (Fig. 1). For this reason, the species *Euryopis californica* Banks, 1904 and *Dipoena tecoja* Levi, 1953 (Hadrotarsinae), as well as *Latrodectus geometricus* C. L. Koch, 1841, *L. mactans* (Fabricius, 1775) and *Steatoda grossa* (C. L. Koch, 1838) (Latrodectinae), were selected as outgroups. As the monophyly of Spintharinae and the relationships among spintharine genera, including their monophyly, are questions addressed in this study, species of each genus of the subfamily were selected as ingroups: *Chrosiothes chirica* (Levi, 1954), *C. portalensis* Levi, 1964, *C. silvaticus* Simon, 1894, *C. tonala* (Levi, 1954), *Episinus amoenus* Banks, 1911, *E. bruneoviridis* (Mello-Leitão, 1948), *E. cognatus* O. P.-Cambridge, 1893, *E. erythrophthalmus* (Simon, 1894), *Spintharus flavidus* Hentz, 1850, (only one species of this genus was available to us), *Stemmops bicolor* O. P.-Cambridge, 1894, *S. ornatus* (Bryant, 1933), *S. orsus* Levi, 1964, *Thwaitesia affinis* O. P.-Cambridge, 1882 and *T. bracteata* (Exline, 1950). Availability of specimens of both sexes, as well as preservation condition, were the main selection criteria. *Moneta* was absent from the analysis because it was not possible to obtain material. For a description of the genus, the works by Nieuwenhuys *et al.* (2011), Saaristo (2006), and Picard-Cambridge (1889–1902), may be consulted. Total number of specimens studied in this work was 131, of which 50 were male and 81 female.

Museums and collections. Specimens were studied from the scientific collections of three institutions, as follows.

AMNH   American Museum of Natural History, New York (Norman I. Platnick).

CNAN Colección Nacional de Arácnidos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (Oscar Francke).

MCZ Museum of Comparative Zoology, Cambridge (Gonzalo Giribet).

Specimen preparation. The epigynum and male pedipalp were removed from specimens with forceps. The epigynum was cleaned using pancreatin (Álvarez-Padilla & Hormiga 2007). Male pedipalps were immersed in 1% potassium hydroxide (KOH) for about one minute at room temperature, and then transferred to distilled water for a rapid expansion (Levi 1961). After that, the structures and the rest of the specimen were revised under a Stemi SV 11 Carl Zeiss stereomicroscope with a 2.5x objective and 30x oculars. The digital photos were taken with a Leica Z16APO-A stereomicroscope and a Leica DFC490 camera, further edited with a Leica Application Suite software and Adobe Photoshop CS®. Characters were searched for, both in male and female specimens. Yet, shape of the plate of the epigynum, size and position of spermathecae, and the number of turns in ducts of spermathecae, were found non informative. Only the number of spermathecae was determined as an informative character in females.

Cladistic analyses. A character matrix containing 19 taxa and 49 characters was built in Excel®, saved as text, then opened and run using PAUP (Swofford 1998). Forty one characters are binary and eight multistate, all were treated as unordered and with equal weights. Searches of the most parsimonious trees were performed using the exact branch-and-bound algorithm. Searches were also performed with TNT (Goloboff 2008) through implicit enumeration. Branch support was estimated through bootstrap (replicates $n = 1000$) and Bremer values (calculated allowing extra steps in additional branch-and-bound searches) with PAUP, on the original unweighted data matrix. A successive weighting analysis, with the rescaled consistency index (RC) as weight (Farris 1969; Carpenter 1988), was run in PAUP. In both analyses, two options of branch collapse were utilized (rule 1, branches collapsed if supported ambiguously; rule 3, branches collapsed with no possible support). A third analysis with implied weights (Goloboff 1993) was performed with TNT ($k = 1$ through 10). Character evolution was visualized with MacClade (Maddison & Maddison 2003)

List of characters

Studied characters are morphological, as well as from behavior and web building. Morphological characters are 20 from the prosoma, nine from the opisthosoma, 13 from male genitalia, one from female genitalia, and one from spinnerets. Five additional characters from behavior were obtained from the literature.

Somatic morphology

01. Distance between lateral eyes: (0) noticeable, eyes separate with respect to each other more than an eye diameter (Fig. 6A, B), (1) eyes adjacent to each other (Fig. 6C, D).
02. Distance between posterior median eyes with respect to lateral eyes: (0) separate from lateral eyes by at least one eye diameter (Fig. 6A, B), (1) adjacent to lateral eyes (Fig. 6C, D).
03. Distance between posterior median eyes: (0) less than an eye diameter, (1) about an eye diameter, (2) two or more eye diameters.
04. Fovea of carapace: (0) shallow, inconspicuous, (1) concave, conspicuous (Fig. 6A, B).
05. Carapace hairiness: (0) sparsely or patchily hirsute, (1) densely hirsute.
06. Color of carapace: (0) pale, (1) dark.
07. Color pattern of carapace: (0) apparently absent, (1) present. Several ingroup taxa, such as *Stemmops*, have markings more or less uniformly distributed throughout carapace. Other taxa have an evenly colored carapace.
08. Carapace height in relation to height of clypeus: (0) subequal, (1) two or three times size of clypeus. Carapace height was measured at its highest point, laterally.
09. Shape of clypeus laterally: (0) concave, (1) straight.
10. Length of chelicera in relation to height of clypeus: (0) subequal, (1) two or three times height of clypeus.
11. Cheliceral base: (0) broad, (1) narrow. In a broad chelicerum its base corresponds to more than half its length (about 60%), while in a narrow chelicerum it corresponds to about half the length of the appendage.
12. Paturon length: (0) short, (1) long. The paturon is the basal segment of the chelicerae (Ubick *et al.* 2005). Forster *et al.* (1990) and Griswold *et al.* (1998) pointed out that chelicerae in Hadrotarsinae are short and do

not reach the coxal endites (state 0; Agnarsson 2004, fig. 5C). In all other taxa the paturon overpasses coxal endites (state 1).

13. Color of chelicerae: (0) pale, (1) dark.

14. Cheliceral fangs: (0) small and thick, (1) long and slender. The classical hadrotarsine fang is long and slender, reaching from the apex of the shortened paturon to the tip of the palpal endites (Forster *et al.* 1990).

15. Shape of labium: (0) subquadrate, (1) subtriangular. *Dipoena* and *Euryopis* have a distinctly triangular labium.

16. Shape of female palpal claw: (0) attenuate (Agnarsson 2004, figs. 16G, 47E, 58G), (1) palmate (Agnarsson 2004, fig. 9E).

17. Shape of opisthosoma in dorsal view: (0) triangular (Fig. 8E), (1) oval (Fig. 9C), (2) trapezoidal (Fig. 8C).

18. Humps of opisthosoma: (0) absent (Fig. 8A), (1) present (Fig. 8C, E). The opisthosoma of several species of Spintharinae may present humps in a variety of numbers and position, and they will be present over the anterior (e.g., *Chrosiothes tonala* and *C. portalensis*), median (e.g., *Episinus cognatus*) or posterior zone (e.g., *E. amoenus* and *E. erythrophthalmus*), and they may also be absent (e.g., *C. chirica, C. silvaticus, Stemmops bicolor, S. ornatus, S. orsus, Spintharus flavidus, Thwaitesia affinis* and *T. bracteata*).

19. Color pattern of opisthosoma in dorsal view: (0) spotted or with points (Fig. 8D), (1) leaf-like and spotted (Fig. 8B), (2) homogenous (Fig. 10D). As pointed out by Agnarsson (2004), the patterns of tone and color of the opisthosoma in different species of theridiids, particularly in Spintharinae, are difficult to code into discrete characters.

20. Longitudinal band of silver spots in dorsal view of opisthosoma: (0) missing, (1) present (Figs. 9D, 10A).

21. Hourglass-shaped red mark on venter of opisthosoma: (0) missing, (1) present.

22. Opisthosoma position in relation to location of pedicel in lateral view: (0) inclined (Agnarsson 2004, fig. 94A–D), (1) straight (Agnarsson 2004, fig. 43A). This character refers to the relative position of the insertion of the pedicel on the opisthosoma. For instance, the pedicel may insert relatively close to the epigynum (Agnarsson 2004), so that in *Chrosiothes, Thwaitesia, Spintharus,* and *Stemmops,* opisthosomas appears inclined or higher, while in *Episinus* the opisthosoma appears straight (pedicel farther from epigynum).

23. Widest portion of opisthosoma in dorsal view: (0) anterior (Fig. 9B, C), (1) middle (Fig. 8F), (2) posterior (Fig. 8D, E).

24. Length of leg I in relation to length of leg IV: (0) subequal, (1) leg I longer than leg IV.

25. Arrangement of flat-tipped sensory setae of tarsus I: (0) ungrouped (Agnarsson 2004, figs. 26G, 84F), (1) grouped (Agnarsson 2004, fig. 6B). In Hadrotarsinae, modified flat-tipped setae are arranged close together along the ventral margin of tarsus I (state 1); all other taxa have such setae evenly and sparsely distributed on tarsus I (state 0).

26. Dorsal margin of the comb bristles in tarsus IV: (0) straight (Agnarsson 2004, fig. 84E), (1) notched (Agnarsson 2004, fig. 70D). Spintharines have peculiar tarsal comb bristles. Viewed dorsally, the distal part is somewhat ladderlike, having distinct acute dorsal notches, particularly at the very tip.

27. Outer lateral tubercle on patellae I–IV: (0) inconspicuous, (1) conspicuous.

28. Colulus: (0) absent, (1) present.

29. Number of colular setae: (0) two, (1) three or more.

Male genitalia

30. Shape of cymbium of pedipalp: (0) oval, (1) sickle, (2) triangular. Several traits of the cymbium have been considered as phylogenetically informative (Agnarsson *et al.* 2007). However, this character refers to its general shape, which is herein proposed as a phylogenetic character.

31. Cymbial hood shape: (0) hook (Fig. 7A), (1) half moon (Fig. 7B), (2) hat (Fig. 7C). The cymbial hood in theridiids is variable in shape and tends to be small. In Latrodectinae and Hadrotarsinae the cymbial hood has an extension in the shape of a hook, although in *Latrodectus* the cymbium itself is highly modified and the hood appears to be reduced or absent. In Spintharinae, the hood is narrow and takes the shape of a half moon. However, in *Spintharus* the hood is more developed and such state is herein described as a hat.

32. Alveolar cavity of cymbium: (0) non sclerotized (Fig. 7E), (1) sclerotized (Fig. 7D). Of all studied taxa, only *Thwaitesia* has a sclerotized alveolar cavity of cymbium. This character, the deepest area of the cymbium (which is a concave structure), may be observed dorsally in cleared specimens, which avoids having to remove sclerotized structures of the palp, and their potential damage.

33. Borders of the base of embolus: (0) non lobate (Fig. 7G), (1) lobate (Fig. 7F). Spider literature is not specific

regarding parts of the embolus. For this analysis, it is divided in two portions: a generally broader, variously shaped base and a longer, thin flagellum. This character refers to the borders of the base of the embolus, which may be unmodified (state 0), or present large or smaller folds (state 1).

34. Arrangement of flagellum of embolus within cymbium: (0) without exceeding limits of cymbium (Fig. 7F), (1) exceeding limits of cymbium (Fig. 7G). The flagellum of embolus may surpass the edge of the cymbium (e.g., *Latrodectus*, *Stemmops*, *Episinus*, *Thwaitesia*, *Spintharus,* and *Chrosiothes*), or in other cases, it remains contained within the limits of the cymbium (e.g., *Dipoena* and *Euryopis*).

35. Length of flagellum of embolus: (0) without exceeding the base of embolus, (1) exceeding the base of embolus (Fig. 7F, G). The length of the flagellum is variable. In some cases the flagellum is long and goes beyond the base of embolus, from a short distance to several coils, while in other cases it is short and does not exceeded the base.

36. Arrangement of flagellum: (0) straight, (1) suboval to rounded, (2) spiral. The flagellum of embolus may consist of a simple bar-like, straight structure (state 0), passing by a short, yet circle-forming structure (state 1), reaching an extremely-coiled, spiral arrangement (state 2).

37. Shape of base of embolus: (0) entire, (1) lobed. The embolic base is variable in shape. However, theridiid species may be generally grouped in two main categories according to the contour of this structure.

38. Sperm duct trajectory of embolus: (0) counter-clockwise, (1) clockwise.

39. First loop of the sperm duct: (0) not constricted, (1) constricted.

40. Shape of conductor base: (0) entire (Agnarsson 2004, figs. 13D, 17F, 52C, D), (1) grooved (Agnarsson 2004, figs. 10A, 28D, 69B). The conductor is a strong character helpful to recognize species (Agnarsson *et al.* 2007). The latrodectine conductor base is hollow and forms a groove into which a hook on the embolus base loosely fits (Agnarsson 2004).

41. Width of conductor distal portion: (0) width subequal to base, (1) enlarged with respect to base.

42. Conductor folding: (0) simply folded (Agnarsson 2004, figs. 46B, 69B, 83B), (1) complexly folded. The spintharine conductor is large and complexly folded, unlike the conductor of any other theridiids.

Female genitalia

43. Spermathecae number: (0) two pairs, (1) one pair.

Spinnerets

44. Spinneret sclerotized ring: (0) absent, (1) present.

Behavior

45. Web architecture pattern: (0) general or missing architecture (Eberhard *et al.* 2008, figs. 6C, 7A–C), (1) specific or unique architecture (Eberhard *et al.* 2008, fig. 10B). Hadrotarsines are wandering ant specialists, so they do not build a prey-catching web (Benjamin & Zschokke 2003). As a general attribute, theridiids (e.g., *Latrodectus* and *Steatoda*) build irregular webs, which may be considered the ancestral web-building pattern (state 0). Other genera appear to depart from the generalized pattern, and they make variously reduced or modified webs, for instance *Episinus*, *Spintharus*, *Thwaitesia*, and *Chrosiothes* (state 1).

46. Web shape: (0) irregular or undetermined (Eberhard *et al.* 2008, fig. 6B), (1) "H"-like (Eberhard *et al.* 2008, fig. 10B), (2) sheet-like (Eberhard *et al.* 2008, figs. 9D, E). Some theridiids (e.g., *Latrodectus* and *Steatoda*) build irregular webs. Other genera make simple line webs, either an H-shaped web with two gumfoot lines (*Episinus* and *Spintharus*) or a few presumably nonsticky lines (*Thwaitesia*), or a simple sheet web with knock-down threads as in *Chrosiothes* (Agnarsson 2004).

47. A peripheral retreat: (0) absent, (1) present.

48. Egg sac outermost fibers: (0) densely spun (Agnarsson 2004, fig. 88A, E, G), (1) loosely woven (Agnarsson 2004, fig. 88C). It is clear that the egg sac webs are sometimes complex, and distinct from prey capture webs (Agnarsson 2004). Egg sacs themselves are also diverse and are useful in distinguishing species in some theridiids (Eberhard *et al.* 2008). In at least some spintharines the outermost fibers of the egg sac are loosely woven, such as in *Thwaitesia* and *Episinus*, compared to many other theridiids where all fibers are densely spun and thus the egg sac surface appears smooth (Agnarsson 2004).

49. Mirmecophagy: (0) present, (1) absent. Most theridiids are generalists on whatever prey their web catches. However, some are specialists such as *Euryopis* and *Dipoena*, which are wandering predators of ants.

TABLE 1. Data matrix of 19 species and 49 morphological characters for the analysis of Spintharinae relationships. Missing data and not comparable states are coded with "?".

Taxa	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Dipoena tecoja	1	0	0	0	0	0	0	1	1	0	1	0	0	1	1	1	1
Euryopis californica	1	0	0	0	0	1	0	1	1	0	1	0	1	1	1	1	0
Latrodectus mactans	0	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	1
L. geometricus	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	1
Steatoda grossa	1	0	0	1	1	0	0	0	0	1	0	1	1	0	0	0	1
Stemmops bicolor	1	1	2	0	0	0	1	0	1	0	1	1	0	0	0	0	1
S. ornata	1	1	2	0	0	0	1	0	1	0	1	1	0	0	0	0	1
S. orsus	1	1	2	0	0	0	1	0	1	0	1	1	0	0	0	0	1
Episinus cognatus	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1
E. amoenus	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2
E. bruneoviridis	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1
E. erythrophthalmus	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2
Thwaitesia affinis	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1
T. bracteata	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Spintharus flavidus	1	0	2	0	0	0	0	0	0	0	1	1	0	0	0	0	1
Chrosiothes tonala	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2
C. chirica	1	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	1
C. portalenis	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2
C. silvaticus	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1

TABLE 1. (Ccontinued)

Taxa	Characters																	
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Dipoena tecoja	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Euryopis californica	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Latrodectus mactans	0	2	0	1	0	0	1	0	0	0	1	1	1	?	0	1	1	1
L. geometricus	0	0	0	1	0	0	1	0	0	0	1	1	1	?	0	1	1	1
Steatoda grossa	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	1	1
Stemmops bicolor	0	?	0	0	0	0	0	0	1	?	0	0	?	1	0	1	1	1
S. ornata	0	2	0	0	0	0	0	0	1	0	0	0	?	1	0	1	1	1
S. orsus	0	0	0	0	0	0	0	0	1	?	0	0	?	1	0	?	?	?
Episinus cognatus	1	0	0	0	1	1	1	0	1	0	0	0	0	1	0	1	1	1
E. amoenus	1	0	0	0	1	2	1	0	1	0	0	0	?	1	0	1	1	1
E. bruneoviridis	0	0	0	0	1	2	1	0	1	0	0	0	?	1	0	1	1	1
E. erythrophthalmus	1	0	0	0	1	2	?	0	1	0	0	0	0	1	0	1	1	1
Thwaitesia affinis	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1
T. bracteata	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1
Spintharus flavidus	0	0	0	0	0	0	1	0	1	0	0	0	0	2	0	1	1	1
Chrosiothes tonala	1	1	0	0	0	0	0	0	1	1	0	0	2	1	0	1	1	1
C. chirica	0	1	0	0	0	0	0	0	1	1	0	0	2	1	0	1	1	1
C. portalenis	1	1	0	0	0	0	0	0	1	1	0	0	2	1	0	1	1	1
C. silvaticus	0	1	0	0	0	0	0	0	1	1	0	0	2	1	0	1	1	1

......continued on the next page

TABLE 1. (Ccontinued)

Taxa	Characters													
	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Dipoena tecoja	0	0	0	0	0	0	0	0	0	0	0	?	?	0
Euryopis californica	0	0	0	0	0	0	0	0	0	0	0	?	?	0
Latrodectus mactans	2	1	1	1	1	0	0	1	0	0	0	1	?	1
L. geometricus	2	1	1	1	1	0	0	1	0	0	0	1	0	1
Steatoda grossa	1	1	1	1	1	0	0	1	0	0	0	1	?	1
Stemmops bicolor	1	0	1	0	0	1	1	1	1	0	0	0	?	1
S. ornatus	1	0	1	0	0	1	1	1	1	0	0	0	?	1
S. orsus	?	0	?	?	0	1	1	1	1	0	0	0	?	1
Episinus cognatus	1	0	1	0	0	1	1	1	0	1	1	0	1	1
E. amoenus	1	0	1	0	0	1	1	1	0	1	1	0	1	1
E. bruneoviridis	1	0	1	0	0	1	1	1	0	1	1	0	1	1
E. erythrophthalmus	1	0	1	0	0	1	1	1	0	1	1	0	1	1
Thwaitesia affinis	1	0	1	0	0	1	1	1	0	1	1	0	1	1
T. bracteata	1	0	1	0	0	1	1	1	0	1	1	0	1	1
Spintharus flavidus	1	0	1	0	0	1	1	1	0	1	1	0	?	1
Chrosiothes tonala	1	0	1	0	0	1	1	1	0	1	2	0	?	1
C. chirica	1	0	1	0	0	1	1	1	0	1	2	0	?	1
C. portalenis	1	0	1	0	0	1	1	1	0	1	2	0	?	1
C. silvaticus	1	0	1	0	0	1	1	1	0	1	2	0	?	1

Results

Trees. We obtained 12 most parsimonious trees (L = 70, CI = 0.814, RI = 0.892, RC = 0.726) with PAUP, and 10 with TNT, in both cases with collapse option 3. Two trees were found with both programs under collapse option 1. Computing a strict consensus tree from the 12, 10, or two trees obtained from the above searches, yields the same topology. All genera emerged as monophyletic. In the strict consensus tree, *Stemmops* is sister to a clade that includes all other ingroup genera (Fig. 2), the latter with their relationships unresolved. Bootstrap and Bremer support values (Fig. 3), respectively, are high for the Spintharinae clade (78, 5), while the values for the genera that conform this subfamily are different, yet all on the high side: *Stemmops* (98, 3), *Episinus* (83, 2), *Thwaitesisa* (94, 2), and *Chrosiothes* (89, 3). The ingroup clade with the polytomy (*Episinus + Thwaitesia + Spintarus + Chrosiothes*) has a rather weak support value (54, 1). When a successive weighting analysis is performed, reweighting all characters with their rescaled consistency index (RC), six trees are obtained with collapse option 3, and this number is stable if additional reweight runs are performed. A similar analysis under collapse option 1 yields a single tree. Both, the strict consensus tree and the single tree, have the same topology (Fig. 3). The latter topology maintains *Stemmops* as sister to the rest of Spintharinae. However, within the latter group, now *Chrosiothes* is sister to the remaining genera, which form a polytomy (*Episinus + Spintharus + Thwaitesia*). In a third analysis under implied weights (k = 1, 4, 5, 7, 8, and 10), either as a strict consensus of two trees (k = 1, 4, 5, 7) or as a single tree (k = 8 and 10), results were equivalent to the original topology from unweighted parsimony (Fig. 2). Within the *k* value range selected, two other topologies were obtained. One (k = 2, 3, 9) that was non consistent with the reweighted tree (Fig. 4), and a second one (k = 6), which was logically consistent (Fig. 5). Both, of course, were consistent with the original unweighted tree (Fig. 2).

Groups. The monophyly of Spintharinae was corroborated (Fig. 2) (it should be noted that Agnarsson (2004) did not include *Chrosiothes*, and *Stemmops* was placed within Pholcommatinae). The monophyly of Spintharinae is supported by four synapomorphies: the dorsal margin of the comb bristle in the tarsus IV notched (character 26,
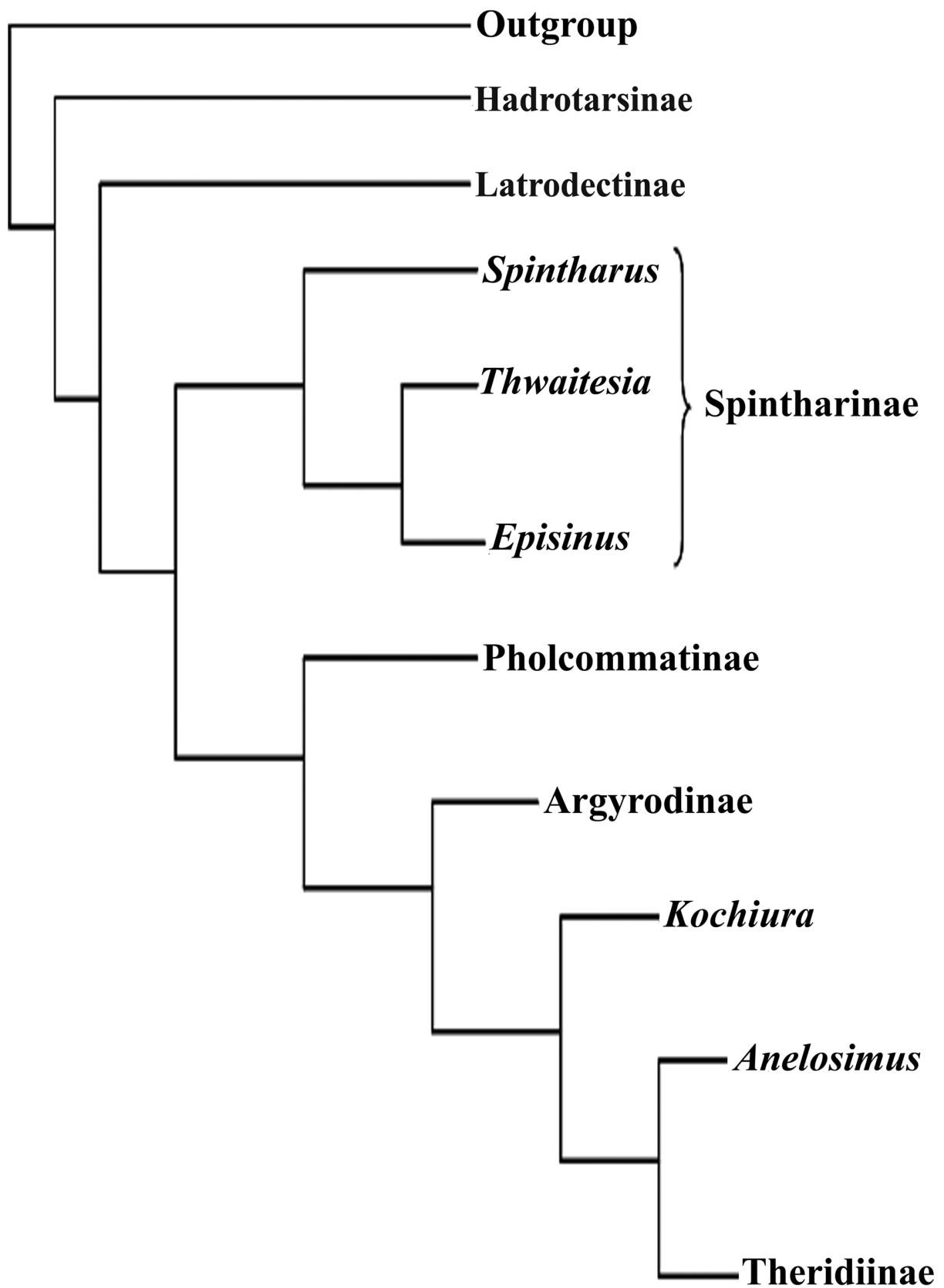
FIGURE 1. Phylogenetic relationships of Theridiidae (modified from Agnarsson 2004).
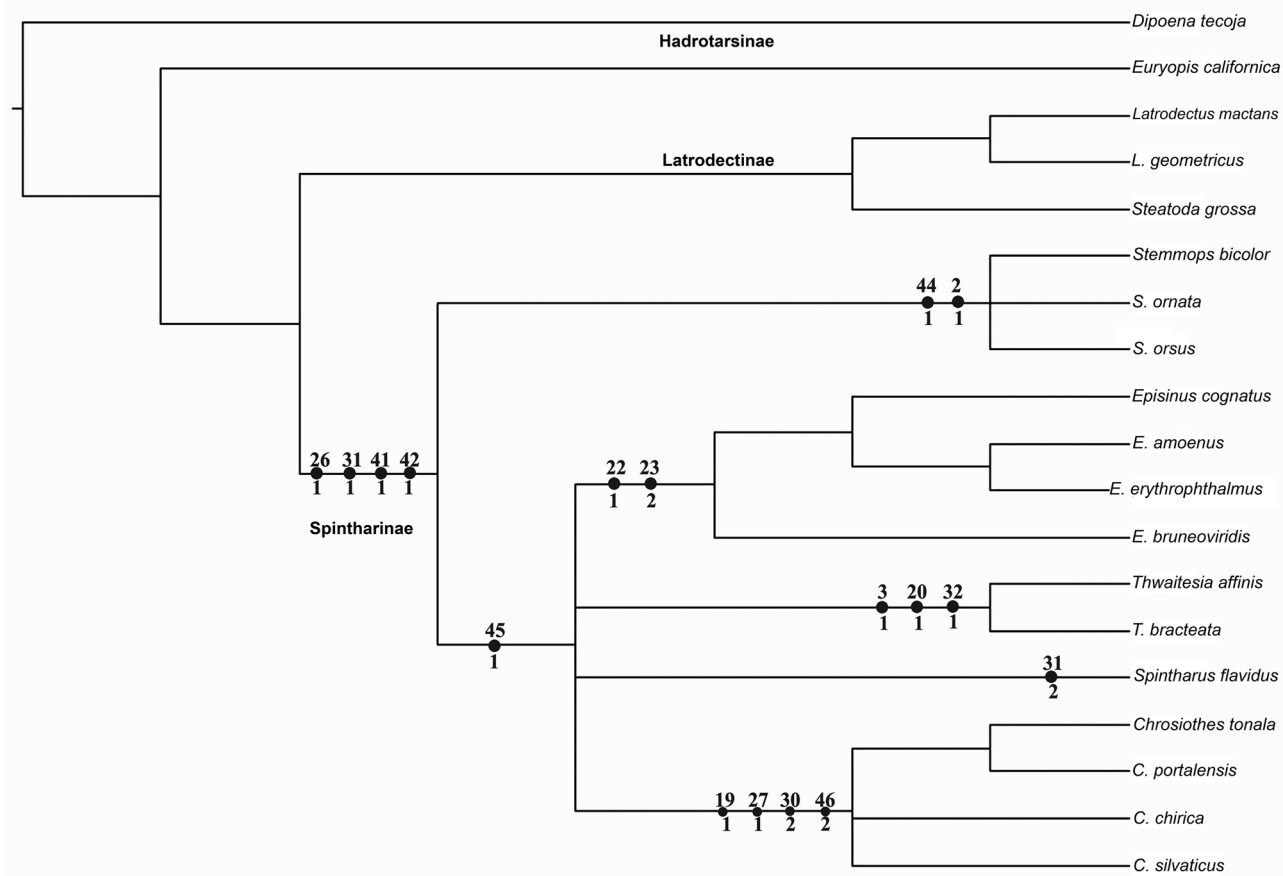
FIGURE 2. Strict consensus tree from the unweighted analysis. The same topology was obtained from 12 (PAUP, branch collapsing rule 3) and two (TNT, branch collapsing rule 1) equally most parsimonious trees (spintharine synapomorphies with character numbers above and character states below).

state 1) (Agnarsson 2004, fig. 84E), the cymbial hood in a half moon shape (character 31, state 1) (Fig. 7B), the distal portion of conductor enlarged (character 41, state 1) (Agnarsson 2004, fig. 46A–D), and a complexly folded conductor (character 42, state 1) (Agnarsson 2004, fig. 90F). The monophyly of the clade comprising *Episinus + Chrosiothes + Spintharus + Thwaitesia* is supported by behavioral character 45 (state 1) (Eberhard *et al.* 2008, figs. 8A–E, 10A–C), presence of a specific pattern of architecture of the web (Agnarsson 2004). All other genera build undifferentiated webs, or do not build webs at all, such as in *Stemmops* (Levi 1955). The monophyly of the ingroup genera is also supported, as follows: *Stemmops* (character 2, state 1, posterior median eyes adjacent to lateral eyes (Fig. 6C–D); character 44, state 1, sclerotized ring present around spinnerets) (Agnarsson 2004, fig. 63B, 74A); *Episinus* (character 22, state 1, straight opisthosoma in relation to location of pedicel; character 23, state 2, posterior portion of opisthosoma in dorsal view, widest) (Fig. 8D–E); *Thwaitesia* (character 3, state 1, an eye diameter for the distance between posterior median eyes; character 20, state 1, a longitudinal band of silver spots in dorsal view of opisthosoma, (Fig. 9D, 10A); character 32, state 1, sclerotized alveolar cavity of cymbium) (Fig. 7D); *Spintharus* (possibly character 31, state 2, hat-like cymbial hood shape, as only one species was included in the analysis) (Fig. 7C); and *Chrosiothes* (character 19, state 1, a leaf-like and spotted color pattern of dorsum of opisthosoma (Fig. 8A–C); character 27, state 1, outer lateral tubercle on patella 1–4 conspicuous; character 30, state 2, a triangular shape of cymbium of pedipal; character 46, state 2, a sheet-like web shape) (Eberhard *et al.* 2008, fig. 8A–E; 9A–E).

The strict consensus of six equally most parsimonious trees (collapsing rule 3 applied), as well as the single tree (collapsing rule 1 applied) from the successive weighting analysis (Fig. 3) contained a new grouping: *Episinus + Spintharus + Thwaitesia*, which may have at least partial support from the following characters: leg I longer than leg IV (character 24, state 1, $ci = 0.5$), "H"-like web shape (character 46, state 1, $ci = 1.0$) (Eberhard *et al.* 2008, fig. 10A–C), and egg sac outermost fibers loosely woven (character 48, state 1, $ci = 1.0$) (Agnarsson 2004, fig. 88C).
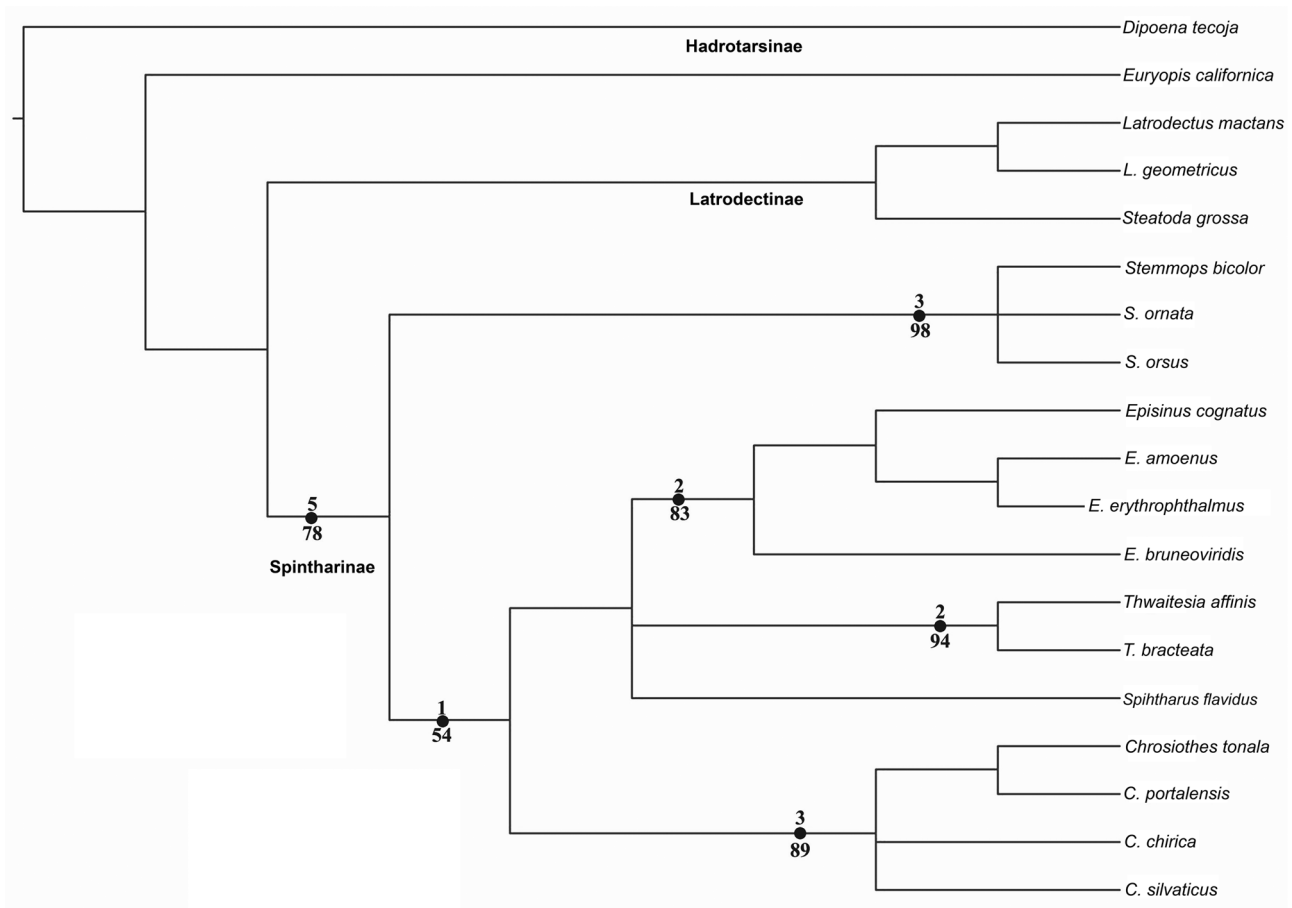
FIGURE 3. Tree from the successive weighting analysis with RC as character weighting function. The same topology was obtained as a strict consensus of six equally most parsimonious trees under branch collapsing rule 3, or as a single tree under branch collapsing rule 1, through PAUP. Bremer support values (above) and ≥50% bootstrap values (below) are from the unweighted analysis.

Of the three topologies obtained from the implied weights analysis, as mentioned above, one is equivalent to the tree from the unweighted analysis under both collapsing rules 1 and 3 (Fig. 2). A second topology corresponds to one of two trees that resulted from the unweighted analysis under rule 1 (Fig. 4). Here, within Spintharinae, excluding *Stemmops*, *Spintharus* emerged as sister to all other genera, and in turn, *Thwaitesia* is sister to *Chrosiothes* + *Episinus*. Only character 10 (state 1; length of chelicerae two or three times the height of clypeus) offers partial support to this topology, as it supports only *Chrosiothes* + *Episinus* (e.g., no potential support was found for *Thwaitesia* + *Chrosiothes* + *Episinus*). Moreover, the topology is logically inconsistent with that of the successive weighting analysis (Fig. 3). Finally, a third topology corresponded to the second of the two trees that resulted from the unweighted analysis under rule 1 (Fig. 5). Here, *Spintharus* was sister to *Thwaitesia* + *Episinus*, this topology is in agreement with the successive weighting analysis. Also, characters 24 (state 1; leg I longer than leg IV) and 46 (state 1; an "H"-like web shape) offer support for the grouping *Spintharus* + *Thwaitesia* + *Episinus*, while character 48 (state 1; a loosely woven outermost fibers of the egg sac) offers support to *Thwaitesia* + *Episinus*. As this topology is fully resolved, it is logically consistent with the successive weighting analysis, corresponds to one of the fundamental cladograms of the unweigthed analysis (under rule 1), and has potential support from three characters, it might be considered the preferred phylogenetic hypothesis. It should be pointed out, that relationships within *Chrosiothes* and *Stemmops* were also resolved.
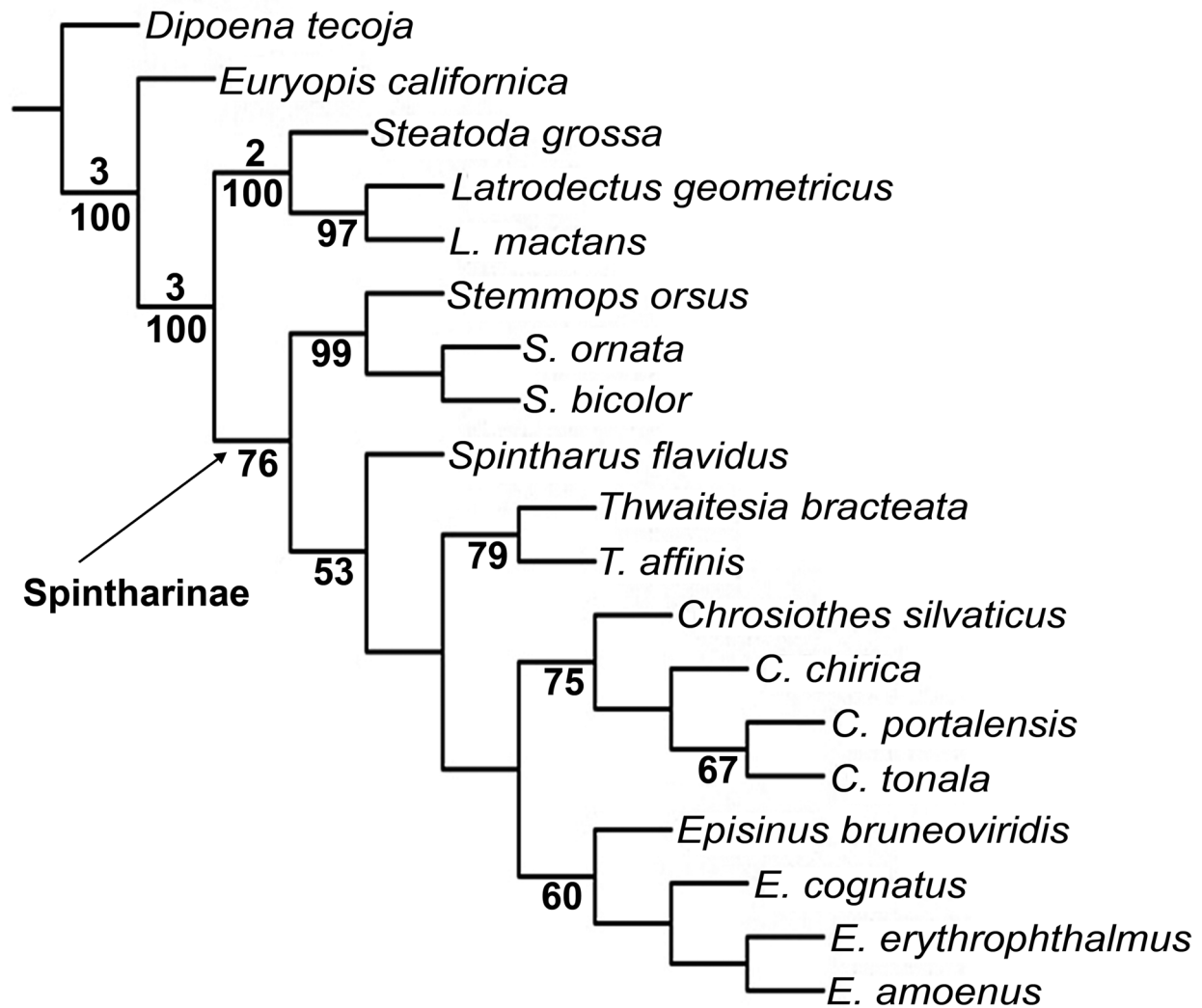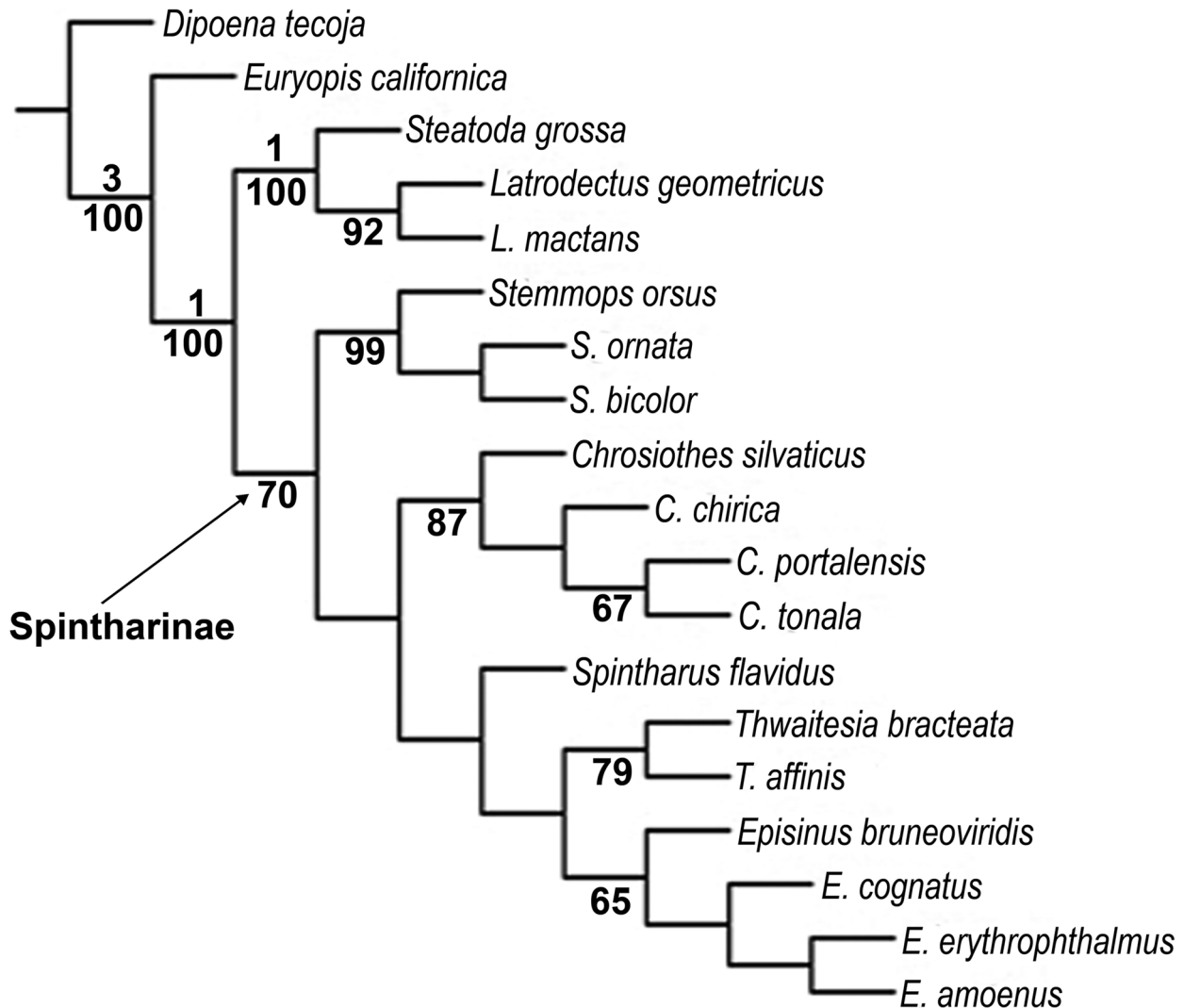
FIGURE 4. Tree from the implied weights analysis (*k* = 2, 3, 9). This topology corresponds to one of the two trees from the unweighted analysis under collapsing rule 1. Bremer support values (above) and ≥50% bootstrap values (below).

Discussion

The results of this study support Spintharinae as a monophyletic group, in agreement with Agnarsson (2004) and Arnedo *et al*. (2004). This finding is of particular importance, because our morphological study included one additional genus, *Chrosiothes* (four species included), that was not part of Agnarsson´s phylogeny. Also, we included three species of *Stemmops* (different to the one used in Agnarsson´s study), whose position in supported within Spintharinae, rather than in Pholcommatinae as in Agnarsson´s study. Moreover, we used three more species of *Episinus*, and two different species of *Thwaitesia*, with respect to Agnarsson´s work. Having used one additional genus, as well as several different species relative to the previously analyzed taxa in Agnarsson´s study, makes our phylogeny relevant to support and complement the previous hypothesis of Spintharinae monophyly.

   In addition to the monophyly of Spintharinae, our strict consensus tree from unweighted parsimony (trees *n* = 12 under collapsing rule 3; trees *n* = 2 under collapsing rule 1) had *Stemmops* as sister to all other genera, which in turn formed a polytomy (*Episinus* + *Thwaitesia* + *Spintharus* + *Chrosiothes*). However, all genera represented by two or more species (only *Spintharus* had one species) emerged individually as monophyletic (Fig. 2). In a second analysis, performed with successive weighting of characters (Fig. 3), *Chrosiotes* is sister to *Episinus* + *Thwaitesia* + *Spintharus*, the latter three with unresolved relationships. In summary, our unweighted tree places *Stemmops* as sister to all other spintharine genera. In the successive weighting analysis, *Chrosiothes* is sister to *Episinus* +

Thwaitesia + *Spintharus* (in a polytomy), possibly because its specific pattern of a sheet-like web (character 46, state 2) (Eberhard *et al.* 2008, fig. 8A–E; 9A–E). A potential synapomorphy for the latter group may be a modified web in an "H"-like pattern (character 46, state 1) (Eberhard *et al.* 2008, fig. 10A–C), although each genus appears to have a specific architecture. Further corroboration of these relationships is required, as they emerged from a successive weighting analysis.

FIGURE 5. Tree from the implied weights analysis (k = 6). This topology corresponds to one of the two trees from the unweighted analysis under collapsing rule 1. Bremer support values (above) and ≥50% bootstrap values (below).

As mentioned above, from the implied weight analyses, one topology (k = 6) was preferred (Fig. 5). The reason for this are that it is logically consistent with the tree from the successive weighting analysis, corresponds to one of two of the fundamental cladograms from the unweighted analysis (under collapsing rule 1), it is fully resolved, has potential character support, and its concavity value (k = 6) is not a low value. In agreement with Arnedo *et al.* (2009), within our range of concavity values (k = 1–10), our preferred tree relies on values that tend towards equal weights. That is, k negatively correlates with how strongly homoplasious characters are down-weighted (Arnedo *et al.* 2009). This topology might be considered a suitable working hypothesis from this contribution.

Although there was an intense search for informative characters, it would be important to test potential characters that were not explored here, such as those suggested by Agnarsson (2004): the distribution of setae (over appendages and body), the distribution of sensory organs (trichobothria and slit sensilla), and tarsus IV claws, which may shed light to resolve phylogenetic problems inside Spintharinae. Another source of information that has been underexploited for phylogeny is related to behavioral and web building traits, as very little is known in this

particular subfamily. Besides weakly resolved relationships within Spintharinae (particularly between *Episinus* + *Spintharus* + *Thwaitesia*), another pending issue is an updated diagnosis of the Old World, mostly Asian *Moneta*, the only genus missing in this study. Within Spintharinae, *Chrosiothes* is of special interest to us, as it is under taxonomic revision, son finding support for its monophyly is also an important result of this study.
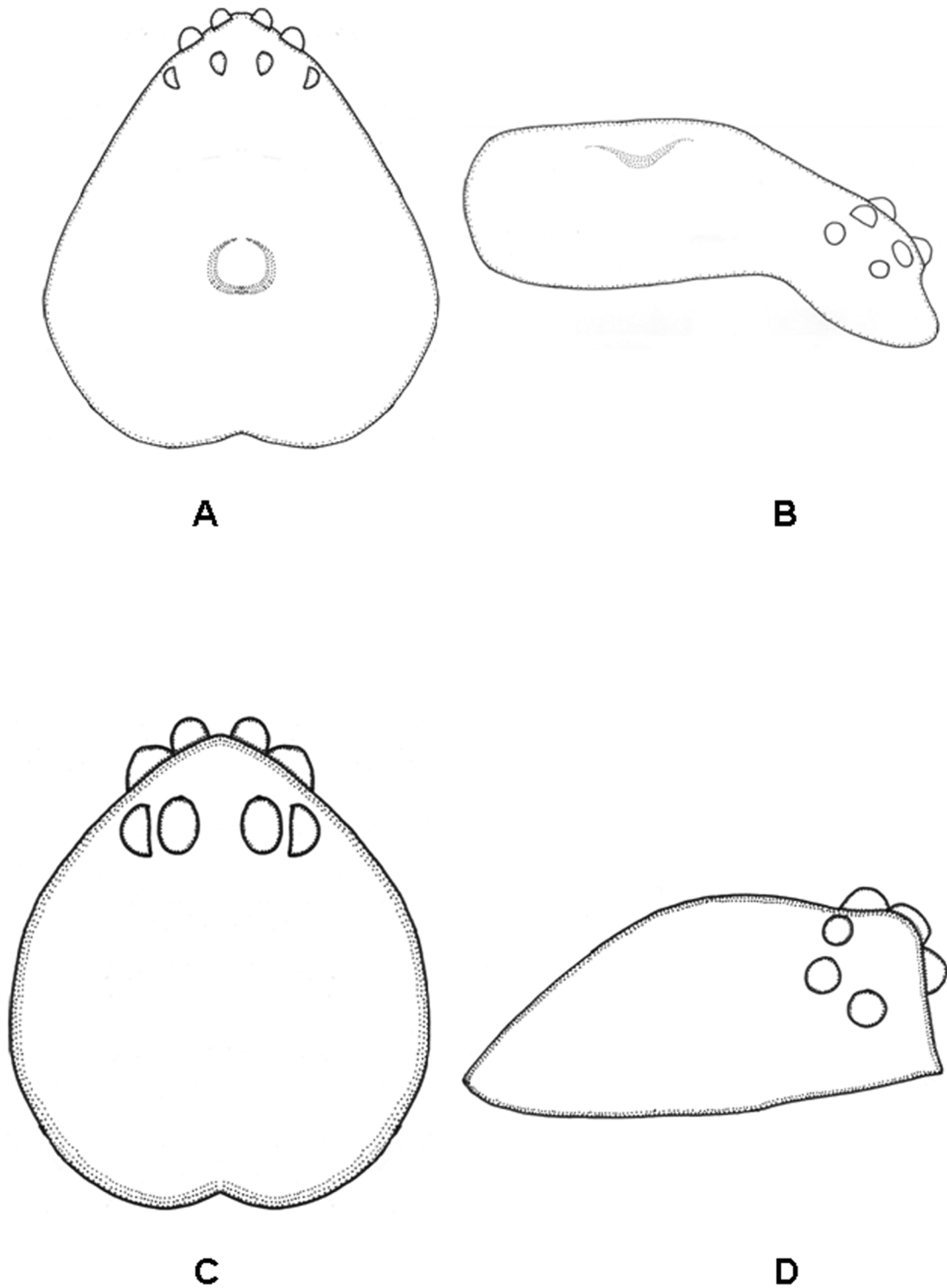

FIGURE 6. Carapace. A, *Latrodectus geometricus* ♀ (dorsal view); B, *L. geometricus* ♀ (lateral view); C, *Stemmops orsus* ♀ (dorsal view); D, *S. orsus* ♀ (lateral view).
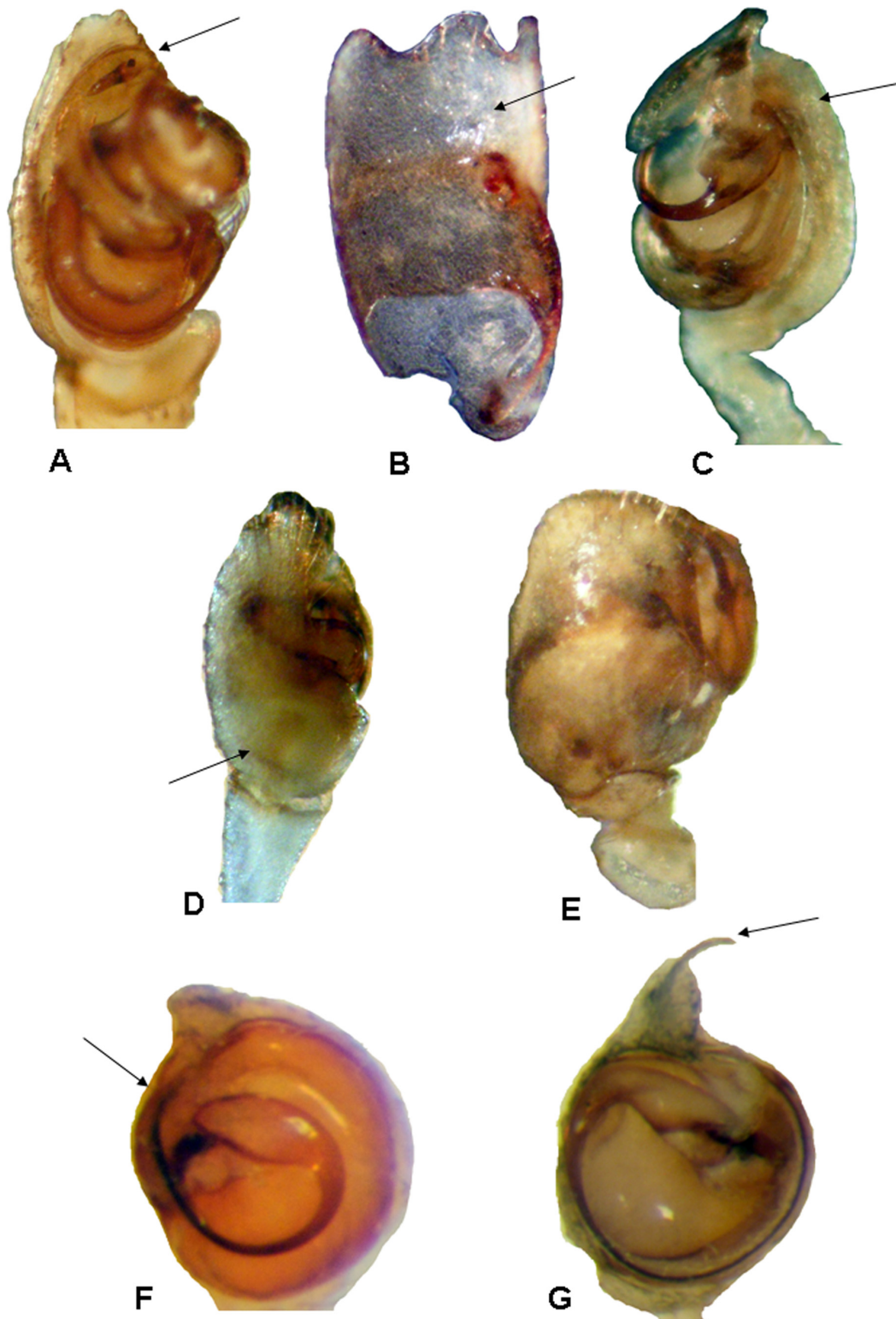
FIGURE 7. Male pedipalp. A, *Steatoda grossa* (left palp, ventral view, arrow = cymbial hood); B, *Episinus cognatus* (left palp, ventral view); C, *Spintharus flavidus* (left palp, ventral view, arrow = cymbial hood); D, *Thwaitesia affinis* (left palp, dorsal view, arrow = alveolar cavity of cymbium); E, *Euryopis californica* (left palp, dorsal view); F, *Chrosiothes portalensis* (left palp, ventral view, arrow = apex of flagellum); G, *C. silvaticus* (left palp, ventral view, arrow = apex of flagellum).

Taxonomy

Key to the genera of Spintharinae
(Modified from Levi & Levi 1962)

1. Opisthosoma straight in lateral view, with median or posterior humps (Fig. 8D–F) . . . . *Episinus*
- Opisthosoma inclined or vertical in lateral view, with humps on anterior, median or posterior position, on all three positions, or missing (Figs. 8A–C, 9A–D, 10A–D). 2
2. Eyes in dorsal view in two parallel rows (Saaristo 2006, figs. 45–47). . . . .*Moneta*
- Eyes in dorsal view with a different arrangement (procurved or recurved) (Fig. 6A–D). 3
3. Posterior median eyes close to laterals (closer to laterals than with each other) (Fig. 6C, D) . . . . *Stemmops*
- Posterior median eyes far from laterals (closer between each other than with respect to laterals) (Fig. 6A, B) 4
4. Opisthosoma higher than wide (in lateral view) (Levi & Levi 1962, fig. 212) . . . .*Thwaitesia*
- Opisthosoma longer than wide (in lateral view) 5
5. Carapace flat and almost circular in outline (in dorsal view) (Levi 1954b, figs. 46,47) . . . . *Spintharus*
- Carapace convex, sometimes highest in thoracic region, subtriangular in outline (in dorsal view) (Levi 1954a, figs. 10, 11, 19– 25) . . . . *Chrosiothes*

Spintharinae Hentz, 1850
(Figs. 8, 9, 10A)

The subfamily Spintharinae is conformed by the genera *Chrosiothes* Simon, 1894; *Episinus* Walckenaer, in Latreille, 1809; *Moneta* O. P.-Cambridge, 1870; *Spintharus* Hentz, 1850; *Thwaitesia* O. P.-Cambridge, 1881 and *Stemmops* O. P.-Cambridge, 1894. Unambiguous synapomorphies include (Agnarsson 2004): conductor huge and folded (Agnarsson 2004, fig. 46A–D; fig. 90F–G), cheliceral base thin (Agnarsson 2004, fig. 84C), colulus small or replaced by two setae (Agnarsson 2004, fig. 70A), tarsal comb bristles with dorsal margin notched (Agnarsson 2004, fig. 84E), web modified (Agnarsson 2004, fig. 97A), and outermost fiber of the egg sac loosely spun (Agnarsson 2004, fig. 88C).

Chrosiothes Simon, 1894
(Figs. 8A–C)

Simon, 1894. Historie Naturelle des Araignées, vol. 1, p. 521. Type species by original designation and monotypy: *C. silvaticus* Simon, 1894, ibid.

Diagnosis. Opisthosoma with a leaf-like and spotted color pattern on dorsum (Fig. 6A, C). In other genera, there exists a pattern made by silver spots that form longitudinal bands (e.g., *Thwaitesia*) (Figs. 9D, 10A), or spotting and points without a defined pattern (e.g., *Episinus*) (Fig. 8D–F). The patella I–IV presents each an outer lateral tubercle conspicuous, while in all remaining spintharinae genera tubercles are inconspicuous (e.g., *Stemmops*) (Figs. 9B–C). The cymbium of pedipalp is triangular in shape, while oval (other Spintharinae) or sickle-shaped (Latrodectinae). A sheet-like web shape is present in *Chrosiothes* (Eberhard *et al.* 2008, figs. 8A–E; 9A–E), while the remaining genera have an irregular or "H"-like web (Eberhard *et al.* 2008, fig. 10A–C). Levi (1954b; 1964b) and Levi and Levi (1962) report the presence of humps in the opisthosoma as a diagnostic character, however, we recognize that some species lack humps (Fig. 8A–B), therefore this character would not be useful to diagnose all *Chrosiothes* species.

Distribution. Mainly in tropical areas. Occurs almost exclusively in the New World but the distribution includes countries like China, Korea, Japan and Taiwan (Platnick 2013).

Material examined. *Chrosiothes chirica*: MEXICO, [Parque Nacional] Desierto de los Leones, [19° 15' 12" N, 99° 19' 51" W], Distrito Federal, 23 April 1946, J. C. & D. L. Pallister, 1 ♀ (AMNH). U. S. A., Utah, Hughes Canyon, 20 May 1934, H. W. Levi, 4 ♂ and 12 immature (AMNH); same data but 20 May 1934, Wilton Ivie, 8 ♂, 4 ♀ and 4 immature (AMNH); Utah, Hughes Canyon, 29 June 1935, H. W. Levi, 4 ♂, 2 ♀ (AMNH); same data but 29 June 1935, H. W. Levi, 1 ♂ y 6 immature (AMNH); Arizona, White Mountains, 17 mi. NE Whiteriver, 8–10 July 1940, J. M. Gertsch, 1 ♀ (AMNH); Arizona, Santa Rita Mountains, Madera Canyon, 16 July 1940, Getrsch &

Hook, 1 ♀ (AMNH); Utah, Mill Creek Canyon 1 to 2 min up, 40° 40′ N 111° 43′ W, 21 August 1941, J. C. Chamberlin, 1 ♀ (AMNH); Arizona, Rustlers Cam, Chiricahua Mountains, 1 June 1952, M. Cazier, W. Gertsch & R. Schrammel, 1 ♂ (holotype) (AMNH); same data but 1 June 1952, M. Cazier, W. Gertsch & R. Schrammel, 2 immature (AMNH); Colorado, Piedra, County of Archuleta, 21 July 1952, L. R. & H. W. Levi, 1 ♂ (AMNH). *Chrosiothes portalensis*: MEXICO, Nayarit, a 15 min. al N de Tepic, 25 July 1954, W. J. Gertsch, 1 ♂ (paratype) (MCZ); Jalisco, [Mpio. La Huerta, San Patricio], Estación de Biología Chamela, [Km 59 Carretera federal 200, Barra de Navidad-Puerto Vallarta], 12 July 1989, S. Guzmán, 1 ♀ (CNAN); same data but 20 August 1989, S. Guzmán, 1 ♀ (CNAN). U. S. A., Arizona, County of Cochise, Chiricahua Mountains, S WRS, Cave Creek Canyon, August 1856, A. F. Archer, 1 ♀ (AMNH); Arizona, Chiricahua Mountains, Rustler Camp, 09 October 1950, W. J. Gertsch, 14 immature (AMNH); Arizona, County of Cochise, Southwestern Research Sta, 5 mi. of West of Portal, 5–15 August 1955, M. J. Gertsch, ♂ (holotype), 1 ♀ (paratype) (AMNH); same data but 1 ♀ (paratype) (MCZ). *Chrosiothes silvaticus*: ECUADOR, Machala, Buenavista 20 km S.E., 11 November 1942, Moore, E., 1 ♂ (MCZ-83505). COSTA RICA, San José, San Antonio de Escazu, 1300 m., W. Eberhard, 1 ♀ (MCZ-83502); Provincia de Cartago, [Town of] Turrialba, 23 July–15 August 1965, A. M. Chickering, 1 ♀ (MCZ-83503). GUATEMALA, [Department Alta Verapaz], [Municipality] Cobán, July 1947, C. & P. Vaurie, 1 ♂ (AMNH). PANAMA, Canal Zone, [Lago Gatún], Barro Colorado Island, 23–30 June 1934, A. M. Chickering, 1 ♀ (MCZ-83880); Canal Zone, Isla Barro Colorado, 16 June–15 July 1934, A. M. Chickering, 3 ♀ (MCZ-83881); Canal Zone, [Lago Gatún], Barro Colorado Island, 25–28 June 1936, A. M. Chickering, 3 ♀, 1 immature (MCZ-83890); same data but 7–9 July 1936, A. M. Chickering, 1 ♀ (MCZ-83889); Canal Zone, 28 July 1936, A. M. Chickering, 2 ♀ (MCZ-83891); El Valle, July 1936, A. M. Chickering, 1 ♂ (MCZ-83509); Barro Colorado Island, [Lago Gatún], Canal Zone, 6–9 August 1936, A. M. Chickering, 1 ♂ (MCZ-83884); Barro Colorado Island, [Lago Gatún], Canal Zone, 23–30 June 1939, A. M. Chickering, 1 ♂ (MCZ-83894); Canal Zone, [Lago Gatún], Barro Colorado Island, 28–31 July 1939, A. M. Chickering, 1 ♀ (MCZ-83883); Canal Zone, [Lago Gatún], Barro Colorado Island, June 1950, A. M. Chickering, 2 ♀ (MCZ-83886); same data but June 1950, A. M. Chickering, 1 ♀ (MCZ-83888); [Barro Colorado Island, Lago Gatún], Canal Zone, Summit, 7–10 July 1950, A. M. Chickering, 1 ♀ (MCZ-83882); Canal Zone, Sumit, 16–17 August 1950, A. M. Chickering, 1 ♂ (MCZ-83885); Canal Zone, [Lago Gatún], Barro Colorado Island, August 1950, A. M. Chickering, 1 ♀, (MCZ-83893); Canal Zone, [Lago Gatún], Barro Colorado Island, 22 July 1954, A. M. Chickering, 1 ♀ (MCZ-83892); [Prov. Chiriquí], [Town] Boquete, 4–11 August 1954, A. M. Chickering, 1 ♀, (MCZ-83508); Canal Zone, [Lago Gatún], Barro Colorado Island, 21 August 1954, A. M. Chickering, 1 ♀ (MCZ-83887). Canal Zone, [Lago Gatún], Barro Colorado Island, May 1964, A. M. Chickering, 3 ♀ (MCZ-83895); Barro Colorado Island, [Lago Gatún], Canal Zone, 17–19 March 1967, A. M. Chickering, 1 ♀ (MCZ-83507); [Canal Zone, Lago Gatún], Barro Colorado Island, 21 June 1973, Y. Lubin, (MCZ-83504); [Barro Colorado Island, Lago Gatún, Canal Zone], A. M. Chickering, 1 ♂, 1 ♀ (MCZ-83896). U. S. A., Florida, County of Hernando, Brooksville, 25 February 1935, Barrows, 1 ♂ (holotype) (AMNH). *Chrosiothes tonala*: MEXICO, Jalisco, [Mpio. La Huerta, San Patricio], Estación de Biología Chamela, [Km. 59 Carretera federal 200, Barra de Navidad-Puerto Vallarta], September 1990, W. Eberhard, 2 ♀ (MCZ); Chiapas, Tonalá, August 1909, 1 ♂ (holotype), 1 ♀ (allotype) (AMNH).

Episinus **Walckenaer, in Latreille, 1809**
(Fig. 8D–F)

Walckenaer, in Latreille, 1809. Genera Crustaceorum et Insectorum, vol. 4, p. 371. Type species by monotypy: *E. truncates* Latreille, 1809, ibid.

Diagnosis. The opisthosoma is straight in relation to the location of the pedicel while in all other spintharine genera it is inclined. Also, the posterior portion of the opisthosoma is widest in dorsal view (Fig. 8D–E), while in the remaining genera the widest portion is anterior or in the middle. An "H"-like architecture of the web is shared with *Thwaitesia* and *Spintharus*. Levi (1954a, 1964a) included the characters horns between the anterior eyes, eyes often on tubercles, and eyes with reddish pigment, as diagnostic characters, all of which we could not observe in the specimens examined.

Distribution. Worldwide, mainly in warmer areas; relatively species rich in North, Central, and South America, poorly known from the Caribbean (Platnick 2013).

Material examined. *Episius amoenus*: MEXICO, Hidalgo, 10–20 miles south of Jacala, 20 July 1956, V. Roth & W. Gertsch, 1 ♂ (AMNH). U. S. A., North Carolina, Buncombe County, Valley 2 1/2 mi S of Black Mt., 2400 m, 23 June 1951, A. F. Archer, 1 ♀ (AMNH). *E. bruneoviridis*: PANAMA, C[anal] Zone, Barro Colorado Island, 3–20 April 1953, A. M. Nadler, 1 ♀ (AMNH). *E. cognatus*: MEXICO, Jalisco, Estación de Biología Chamela, 7 August 1989, S. Guzmán, 1 ♂ (CNAN); same data but 16 August 1989, S. Guzmán, 1 ♂ (CNAN); same data but 29 October 1989, S. Guzmán, 1 ♂ (CNAN); same data but 15 November 1990, S. Guzmán, 2 ♂ (CNAN); same data but 15 November 1990, S. Guzmán, 2 ♂ (CNAN); same data but 02 June 1998, J. L. Castelo, 2 ♀, 3 ♂ (CNAN); same data but 02 September 1998, S. Guzmán, 1 ♀ (CNAN); Jalisco, Mpio. La Huerta, Estación de Biología Chamela, Sendero del Tejón, 19.50501° N, 105.08326° W, 3 October 2010, R. Paredes, G. Montiel-Parra, D. Barrales, G. Contreras, 1 ♀ (CNAN); same data but 4 October 2010, R. Paredes, G. Montiel-Parra, D. Barrales, G. Contreras, 1 ♀ [diurnal collecting] (CNAN). *E. erythrophthalmus*: PANAMA, Canal Zone, Forest Reserve, 4–6 July 1939, A. M. Chickering, 1 ♀, 1 ♂ (AMNH).

Moneta O. Pickard-Cambridge, 1870

O. Pickard-Cambridge, 1870, Proc. Zool. Soc. London, p. 736. Type species by monotypy: *Moneta spiniger* O. Pickard-Cambridge, 1870.

Diagnosis. *Moneta* species may be recognized by having the eyes in dorsal view in two parallel rows (Saaristo 2006).

Distribution. Mostly occur in Asia and Oceania (Platnick 2013).

Material examined. None.

Spintharus Hentz, 1850
(Fig. 9A)

Hentz, 1850. J. Boston Soc. Nat. Hist., vol. 6, p. 283. Type species by monotypy: *S. flavidus* Hentz, 1850, *op. cit.*, p. 284, pl. 10, fig. 8.

Diagnosis. The male palpus presents the cymbial hood in a hat-like shape (Fig. 7C); while the other genera have a cymbial hood as a hook or half moon shape (Fig. 7A–B). The architecture of an "H"-like web is shared with *Thwaitesia* and *Episinus*. Levi and Levi (1962, figs. 203, 204) comment that *Spintharus* may be distinguished because of an opisthosoma longer than wide, widest anterior to middle. Studied specimens had an unpatterned, uniformly pale brown opisthosoma.

Distribution. From the United States to Bolivia and Brazil, with one species found in Pakistan (Platnick 2013).

Material examined. *Spintharus flavidus*. U. S. A., Tennessee, Stony Point, 20 August 1939, R. V. Chamberlin, 1 ♂ (AMNH); (no locality) R. V. Chamberlin, 1 ♀ (AMNH).

Stemmops O. P.-Cambridge, 1894
(Fig. 9B, C)

O. P.-Cambridge, 1894. Biologia Centrali-Americana, Araneidea, vol. 1, p. 125. Type species by monotypy: *S. bicolor* O. P.-Cambridge, 1894, ibid., pl. 17, fig. 5.

Diagnosis. Species of *Stemmops* present the posterior median eyes closer to the lateral eyes (Levi 1955) than between themselves (Fig. 6C, D). In all other spintharines their posterior median eyes are far from the lateral eyes. A sclerotized ring around the spinnerets is exclusive of this genus (Aganarsson 2004, figs. 63B, 74A).

Distribution. Mostly occur in warm parts of America, from U. S. A. to Brazil. Two species are found in China, Japan and Korea (Levi 1964b; Yaginuma 1969; Platnick 2013).

Material examined. *Stemmops bicolor*: U. S. A., Georgia, north of Sylvania, 15 April 1943, 1 ♀ (AMNH). ***Stemmops orsus***: PANAMA, [Province of Chiriquí], [Town] Boquete, 18 August 1950, A. M. Chickering, 1 ♀ (paratype) (AMNH). ***Stemmops ornata***: U. S. A., Ohio, Cantwell Cliffs near Rockbridge, 39° 37 N, 82° 33´ W, 08 August 1935, W. M. Barrows & W. Ivie, 1 ♀ (AMNH).

Thwaitesia O. P.-Cambridge, 1881
(Figs. 9D, 10A)

O. P.-Cambridge, 1881. Proc. Zool. Soc. London, p. 766. Type species by monotypy: *T. margaritifera* O. P.-Cambridge, 1881, op. cit., p. 767, pl. 66, fig. 1.

Diagnosis. The posterior median eyes have a distance between them about an eye diameter. Other spintharine genera present the posterior median eyes separated for less than an eye diameter or twice or more an eye diameter. Dorsally the opisthosoma presents a pigmentation pattern conformed by silver spots that become longitudinal bands (Figs. 9D, 10A). In the rest of genera, pigmentation forms a leaf-like pattern, just spotting, or points with no pattern defined. The male pedipalp cavity is sclerotized, only in this genus, observed dorsally in cleared specimens (Fig. 7D). An "H"-like web architecture is shared with *Episinus* and *Spintharus*. Levi and Levi (1962) comment that *Thwaitesia* is close to *Spintharus* and *Episinus* and that some species are probably intermediate between them.

Distribution. Africa, Australia, Southeast Asia, Indonesia, Caribbean, Central America, South America; probably worldwide in the tropics (Platnick 2013).

Material examined. *Thwaitesia affinis*: BRAZIL, [Municipality Rio de Janeiro], [Town] Petropolis, April 1946, 850 m, H. Sick, 1 ♂ (AMNH). PANAMA, Canal zone, Summit, October 1946, N. L. H. Krauss, 1 ♀ (AMNH); Summit C[anal] Z[one], November 1946, N. L. H. Krauss, 1 ♀ (AMNH). CO-OPERATIVE REPUBLIC OF GUYANA, Rupununi River, near mountains Makavapan, 5 October 1937, W. G. Hassler, 1 ♂ (AMNH). ***Thwaitesia bracteata***: BRAZIL, [Rio de Janeiro], [City] Sumaré, January 1946, 200–300 m, H. Sick, 1 ♂ (AMNH); Rio de Janeiro, [Municipality] Paineiras, 22 January 1959, A. M. Nadler, 5 ♀, 1 ♂ (AMNH). COLOMBIA, [Department] Amazonas, [City] Leticia, February 1956, J. N. Layne, 1 ♀ (AMNH). PARAGUAY, Jaguarazaga, Alto Paraná, 7 ♀, 2 ♂ (AMNH-3721).

Outgroup taxa: specimens examined
(Fig. 10B–D)

Dipoena tecoja: MEXICO, Chiapas, Mpio. Ocosingo, Camino al crucero, 16° 47´ 50.9´´ N, 90° 55´ 00.6´´ W, 133 m, 13 July 2004, J. L. Castelo, 1 ♂, 1 ♀ (CNAN). *Euryopis californica*: MEXICO, Jalisco, Mpio. El Limón, Pueblo San Buenaventura, 19° 45.006´ N, 104° 03.555´ W, 840 m, 03 December 1996, F. Álvarez & J. L. Castelo, 1 ♀ (CNAN); same data but Los Yesos 6.6 km SO, 19° 45.006´ N, 104° 03.555´ W, 840 m, 01 April 1997, F. Álvarez & J. L. Castelo, 1 ♂ (CNAN). *Latrodectus geometricus*: MEXICO, Oaxaca, Mpio. Cuicatlan, Dominguillo, 17° 38.907 N, 96° 54.703 W, 670 m, 18 July 1998, F. Álvarez, J. L. Castelo & C. Durán-Barrón, 2 ♀ (CNAN); Morelos, Cuernavaca, Col. Buenavista, Calle Burciaga # 111, 4 October 1997, T. M. Pérez, 1 ♂, 1 ♀ (CNAN). *Latrodectus mactans*: MEXICO, Morelos, [Mpio.] Palmira, 1950, 1 ♂ (CNAN); Morelos, Mpio. Tlaltizapan de Zapata, Pueblo Ticuman, 18° 45´ 44´´ N, 99° 07´ 09´´ W, 960 m, 24 October 2011, G. Montiel-Parra, 1 ♀ (CNAN). *Steatoda grossa*: MEXICO, Distrito Federal, Del. Miguel Hidalgo, Col. 16 de Septiembre, Poniente 75 # 183, C. P. 11810, 25 April 2001, L. Olguin, 1 ♂ (CNAN); Distrito Federal, Del. Xochimilco, Barrio Xaltocan, Galeana # 2, 21 September 2011, A. López Cortes, 1 ♀ (CNAN).
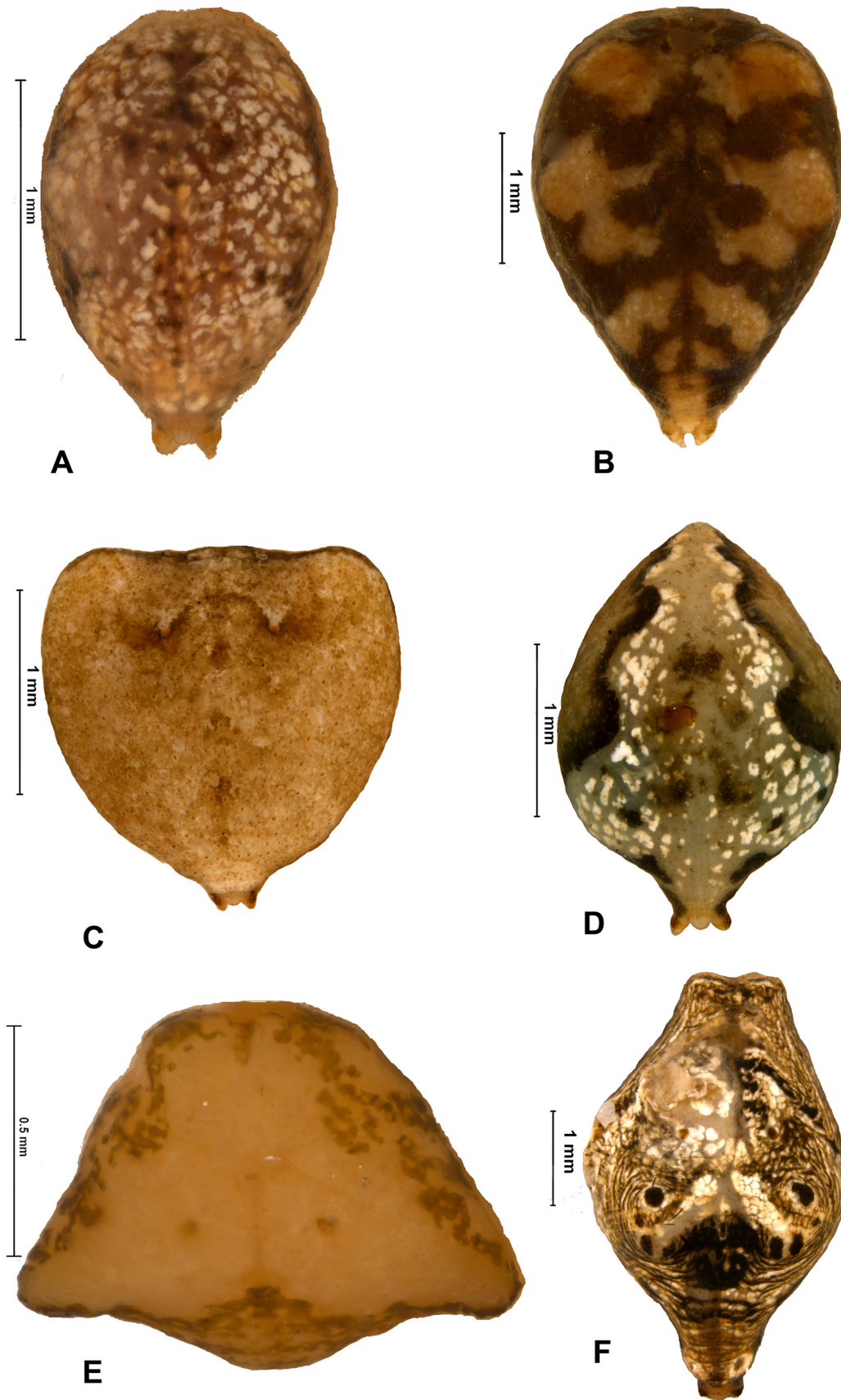
FIGURE 8. Opisthosoma (dorsal view). A, *Chrosiothes chirica* ♀; B, *C. silvaticus* ♀; C, *C. portalensis* ♀; D, *Episinus bruneoviridis* ♀; E, *E. erythrophthalmus* ♂; F, *E. cognatus* ♀.
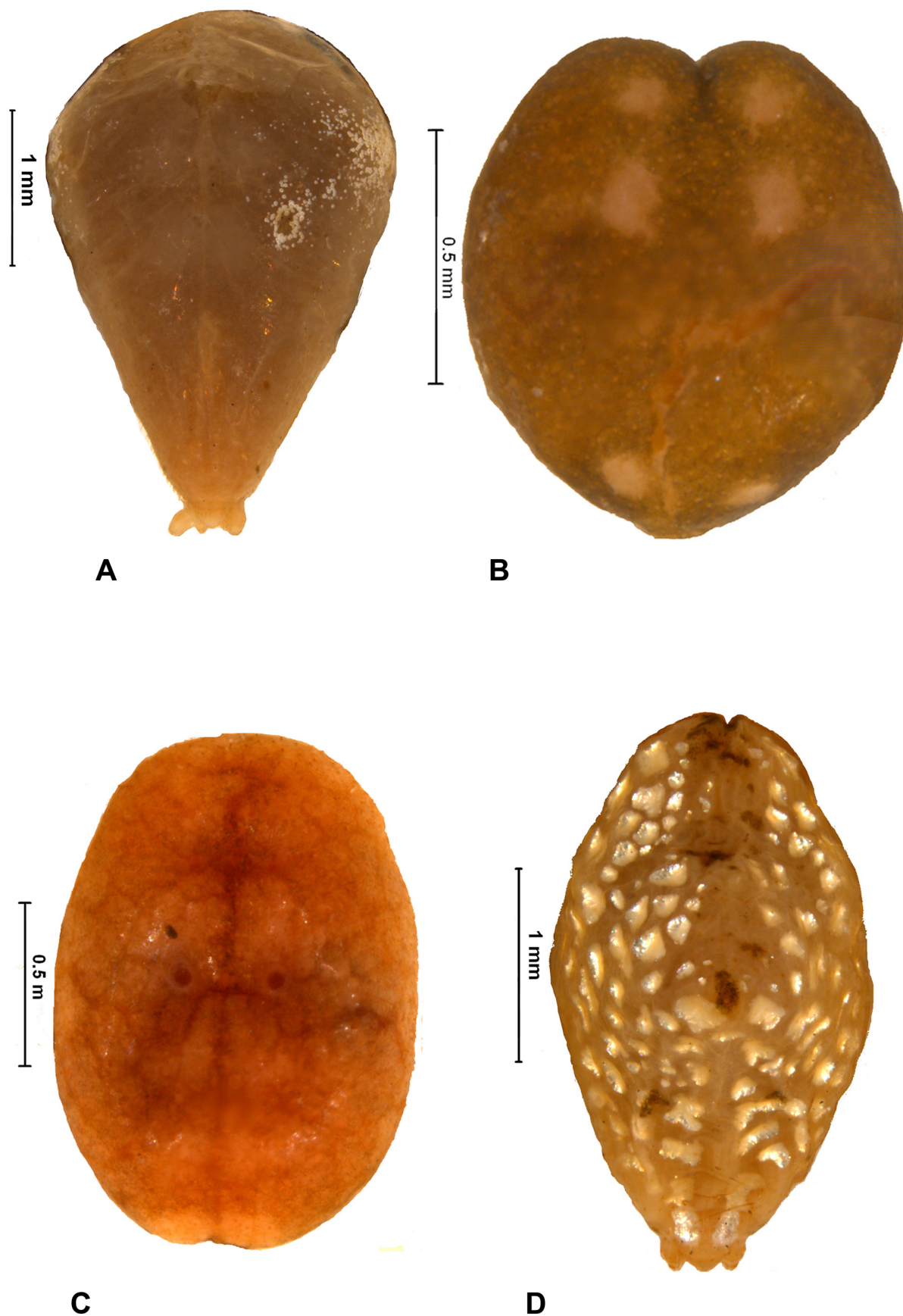
FIGURE 9. Opisthosoma (dorsal view). A, *Spintharus flavidus* ♀; B, *Stemmops orsus* ♀; C, *S. ornata* ♀; D, *Thwaitesia bracteata* ♀.
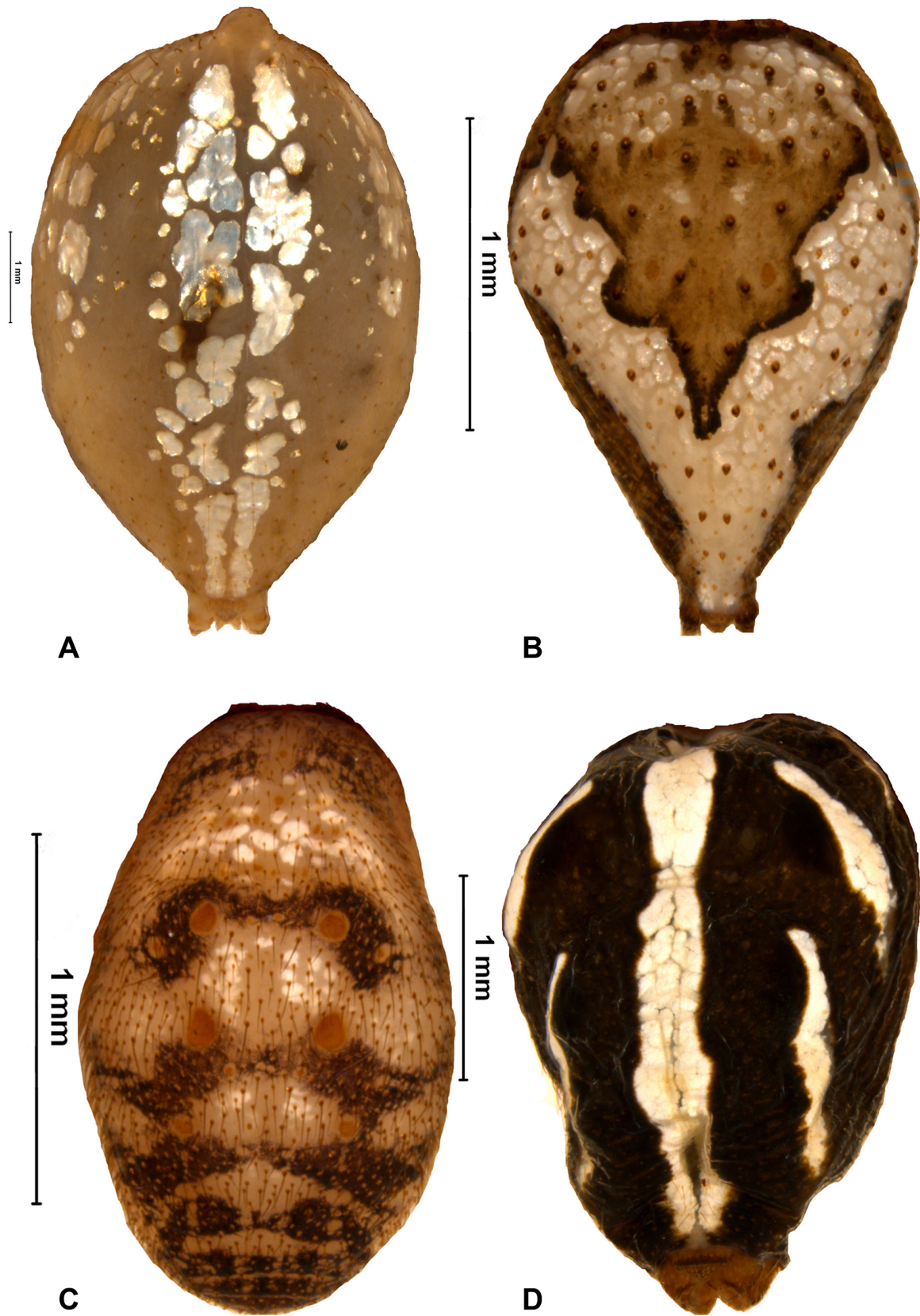
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FIGURE 10. Opisthosoma (dorsal view). A, *Thwaitesia affinis* ♀; B, *Euryopis californica* ♀; C, *Steatoda grossa* ♂; D, *Latrodectus mactans* ♂.

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