Spinneret Spigot Morphology in Synaphrid Spiders (Araneae, Synaphridae), with Comments on the Systematics of The Family and Description of A New Species of SynaphrisSimon 1894 from Spain

Authors: LOPARDO, LARA, HORMIGA, GUSTAVO, and MELIC, ANTONIO

Source: American Museum Novitates, 2007(3556) : 1-26

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2007)3556[1:SSMISS]2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3556, 26 pp., 14 figures, 1 table March 8, 2007

Spinneret Spigot Morphology in Synaphrid Spiders (Araneae, Synaphridae), with Comments on the Systematics of the Family and Description of a New Species of *Synaphris* Simon 1894 from Spain

LARA LOPARDO,[1] GUSTAVO HORMIGA,[2] AND ANTONIO MELIC[3]

ABSTRACT

We describe for the first time the spigot morphology of two synaphrid species (one of each of two synaphrid genera, *Synaphris* and *Cepheia*) as well as the morphology of the respiratory system of *Synaphris*. We also provide a taxonomic description of a new species of *Synaphris* from Spain, including detailed information about its morphology. This new species is known only from males, and it might belong to the so-called *letourneuxi* species group. Some morphological features proposed as synapomorphies for the genus *Synaphris* and/or the Synaphridae are questioned and discussed. Putative synapomorphies proposed here include a distinct constriction on the tarsus-metatarsus joints; a cheliceral keel ending in a strong promarginal cheliceral tooth; scarce number of maxillary setae; distal maxillary setae clavate; and a characteristic palpal morphology, comprising a distinctive tibial morphology, a modified cymbium with two separate areas, a palpal dorsal translucent expansion of the embolar base, a retrolateral paracymbium, a reduced furrow separating the major ampullate field from the piriform field, and the retention of at least one triad spigot in males. Refuted synapomorphies are the metatarsal subdistal anastomosed lyriform organ, the notched tibial trichobothrial base, and the tarsal pseudosegmentation. We also discuss the phylogenetic placement of the family, suggesting a close relationship to the araneoid Cyatholipidae.

[1] Department of Biological Sciences, The George Washington University, 2023 G St. NW, Washington, D.C. 20052, USA (laralo@gwu.edu).
[2] Department of Biological Sciences, The George Washington University), 2023 G St. NW, Washington, D.C. 20052, USA (hormiga@gwu.edu).
[3] Sociedad Entomológica Aragonesa (SEA), Avenida Radio Juventud 37, 50012 Zaragoza, Spain (amelic@telefonica.net).

ISSN 0003-0082

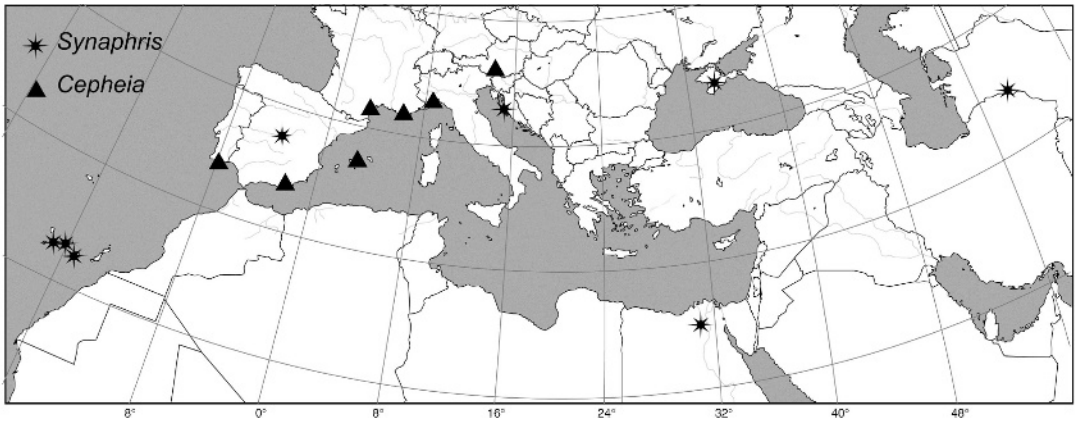


Fig. 1. Map showing the geographic distribution of the described species of *Cepheia* and *Synaphris* around the Mediterranean region in Europe. For the geographic distribution of the recent species from Madagascar, see Miller (in press). For *Synaphris*, each location represents one described species. For *Cepheia*, all locations represent the geographical distribution of *Cepheia longiseta*.

INTRODUCTION

The recently erected araneoid spider family Synaphridae Wunderlich 1986 (Marusik and Lehtinen, 2003, see also Schütt, 2003) comprises two genera of minute spiders: the monotypic *Cepheia* Simon 1894, from southern Europe, and *Synaphris* Simon 1894, with seven species described from the Canary Islands, Croatia, Ukraine, Turkmenistan, and Egypt (fig. 1; Platnick, 2006). Two new *Synaphris* species and a third synaphrid genus from Madagascar are currently being described (Miller, in press). Recent studies (Miller, in press; Marusik et al., 2005; Marusik and Lehtinen, 2003; Schütt, 2003) have proposed putative synapomorphies in support of the monophyly of the family and/or of the genus *Synaphris*. The familial synapomorphies include a cheliceral keel that ends in a single strong prolateral tooth (Wunderlich, 1986, 1995; "tooth-like projection", Schütt, 2003; also "process with pointed tip", Marusik and Lehtinen, 2003); presence of paracymbium; cymbium modified into a rounded lobe; palpal tibia pressed against the cymbial base and with two pits (Marusik and Lehtinen, 2003: 147, fig. 17; see Discussion below); a flattened and transparent extension of the embolic base called lamella; absence of leg spines; tarsi longer than metatarsi; a notched tibial trichobothrial base; anastomosing lyriform organs on subdistal metatarsi (all features above from Marusik and Lehtinen, 2003); embolar and cymbial conductor; and pseudosegmentation of tarsi (Marusik et al., 2005). Most of the features listed above were observed in only one or two *Synaphris* species and generalized for the family. No detailed study of the morphology of *Cepheia longiseta* and of most *Synaphris* species has ever been done, and their spinneret spigot morphology remains undescribed. Given the importance of spigot morphology for reconstructing the cladistic relationships of araneoid families (e.g., Griswold et al., 1998, 2005) the study of this character system should contribute to understanding the phylogenetic position of synaphrids. In this paper we describe for the first time the spigot morphology of two synaphrid species (one of each of two synaphrid genera; see also Miller, in press, for the spinneret spigot morphology of three recently described synaphrid species). We also provide a taxonomic description of a new species of *Synaphris* from Spain, including detailed information about the external morphology and the tracheal system. We discuss some of the morphological features of synaphrids and their potential value as systematic characters. The new species is the first record of the genus *Synaphris* for the Iberian Peninsula. In addition, we report the first records of *Cepheia* from Portugal and the Baleares Islands.

TABLE 1

Length of Individual Segments and Total Length of Left Legs, for Seven Specimens of *Synaphris saphrynis*, n.sp.

Measurements are in millimeters, range in parentheses.

	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
Leg I	0.30 (0.30–0.34)	0.12 (0.12–0.13)	0.25 (0.25–0.28)	0.19 (0.18–0.20)	0.20 (0.20–0.22)	1.05 (1.05–1.15)
Leg II	0.29 (0.28–0.30)	0.12 (0.11–0.12)	0.22 (0.22–0.25)	0.17 (0.17–0.19)	0.20 (0.20–0.22)	1.00 (0.99–1.07)
Leg III	0.25 (0.25–0.29)	0.11 (0.09–0.13)	0.18 (0.17–0.22)	0.16 (0.16–0.18)	0.18 (0.17–0.20)	0.88 (0.88–0.97)
Leg IV	0.30 (0.30–0.35)	0.12 (0.11–0.13)	0.27 (0.27–0.29)	0.19 (0.19–0.20)	0.20 (0.19–0.22)	1.09 (1.09–1.17)

MATERIAL AND METHODS

Methods of study follow Hormiga (2003). Specimens were studied in 75% ethanol using a Leica MZAPO stereomicroscope. For observation of respiratory structures, the abdomens of two specimens were bisected horizontally and digested with SIGMA Pancreatin LP 1750 enzyme complex in a solution of sodium borate, prepared following the concentrations described by Dingerkus and Uhler (1977) as modified in Alvarez Padilla and Hormiga (in prep.). Some of the tracheal system preparations were stained with an aqueous solution of chlorazol black as described in Hormiga (1994). The bisected abdomen was left in the enzymatic solution overnight and at room temperature. After the enzymatic digestion, the specimens were transferred to distilled water for observation. All measurements are in millimeters. Carapace height was measured at the highest point, from the carapace lateral edge, not from the sternum. Abdominal height, length, and width were measured at the maximum points. To account for length variation, measurements are expressed first as the length of the described specimen, then as the range of all observed specimens (in parentheses, table 1). After dissection, palps were cleared in clove oil. Palp drawings were made with a camera lucida attached to a Leica DMRM compound microscope. For SEM images, the specimens were critical-point dried and sputter-coated with gold-palladium. Images were taken with a LEO 1430VP microscope at the Department of Biological Sciences (GWU) SEM facility. Species descriptions and measurements follow Lopardo (2005) and Marusik et al. (2005). Leg formula refers to the relative length of legs. Two legs are considered equally long when their range of variation highly overlaps, even if their averages are slightly different. We comment on and propose some changes in the system of names used by Marusik et al. (2005). Study specimens will be deposited in the American Museum of Natural History (AMNH, New York), the California Academy of Sciences (CAS, San Francisco), the Museum of Comparative Zoology (MCZ, Harvard University), and the Museo Nacional de Ciencias Naturales de Madrid (MNCN, Spain). For abbreviations used through figures and text see appendix 1.

RESULTS

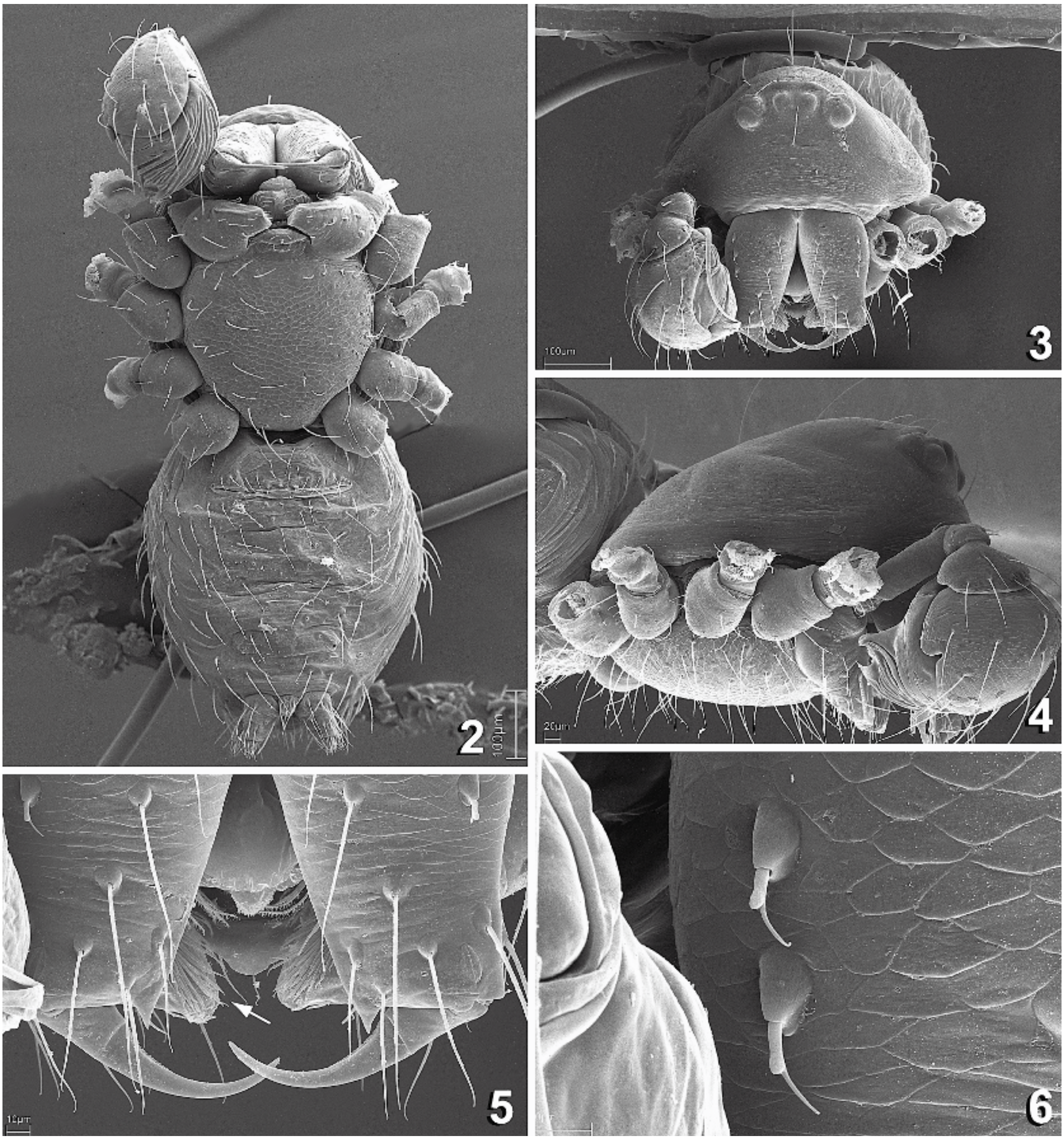
Synaphris saphrynis, new species

figures 1–62

TYPES: 1♂ holotype and 7♂ paratypes from SPAIN: Toledo, Huecas, 29.v.2003, Kleijn et al. col. (30T-395937) (♂ holotype in MNCN-20.02/16523; 4♂ paratypes in MNCN-20.02/16524, 1♂ paratype in AMNH, 1♂ paratype in MCZ, 1♂ paratype in CAS).

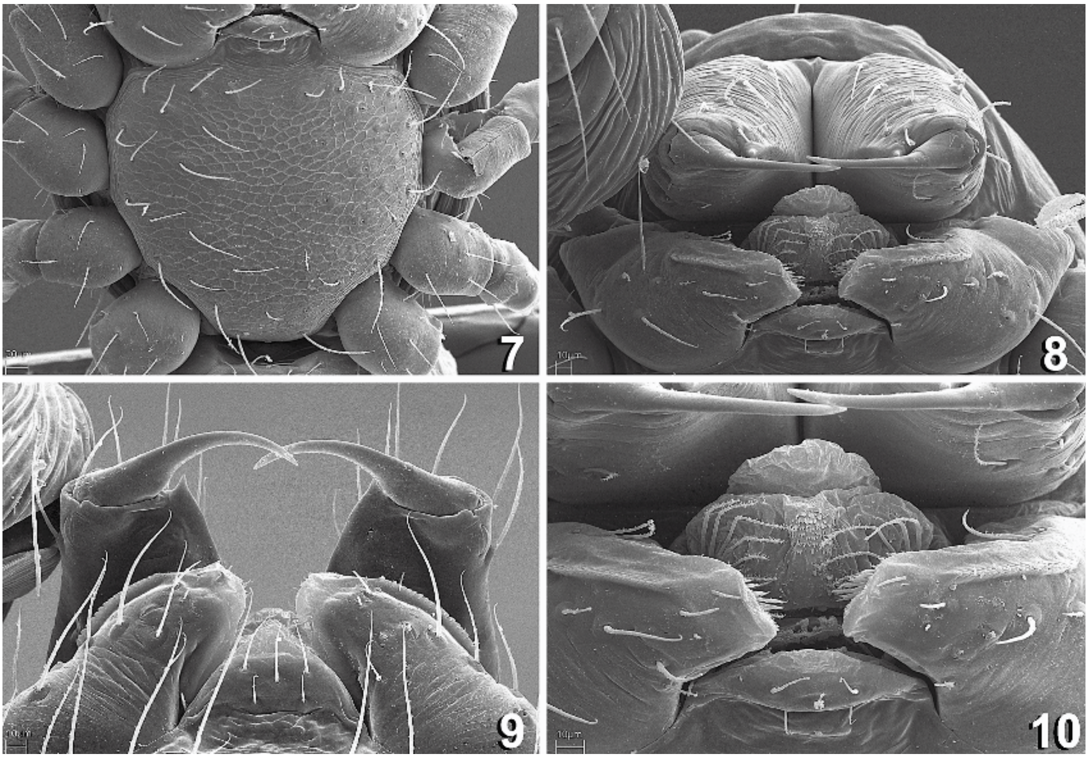
ETYMOLOGY: The species epithet is an arbitrary combination of letters.

DIAGNOSIS: Males of *Synaphris saphrynis*, n.sp. can be distinguished from other *Synaphris* species by the following combination of palpal characters: conductor with tegular groove accompanying the distal portion of the embolus; with two distal apophyses, the ventral one (hereafter "Cap", "subterminal apophysis" of Marusik et al. 2005) clearly bipartite with both tips rounded (i.e., without an irregular border); an embolar membranous expansion ("lamella" of Marusik et al. 2005); width of embolar expansion base 2/5 the width of the expansion (i.e., base of expansion width/expansion width: 0.40).



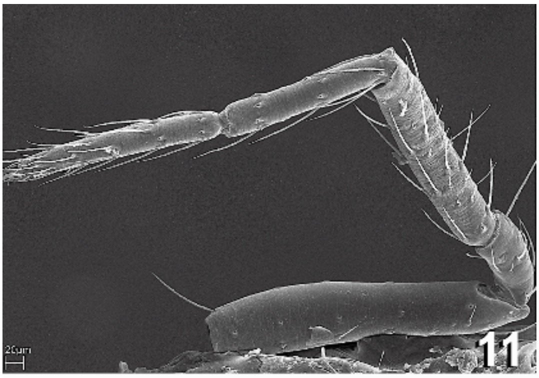
Figs. 2–6. *Synaphris saphrynis*, n.sp. Male paratype. **2.** Ventral view; **3.** Frontal view; **4.** Cephalothorax, lateral view; **5.** Detail of mouthparts, frontal view, arrow to clavate maxillary setae; **6.** Detail of cheliceral prolateral short hairs.

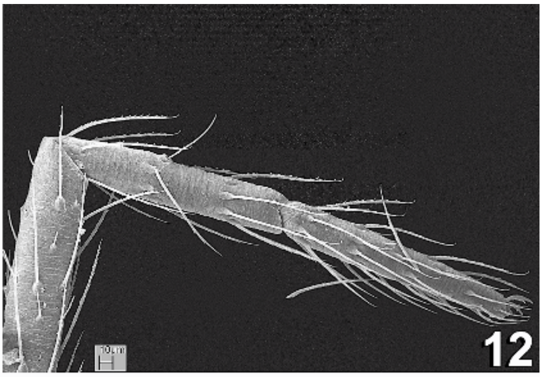
DESCRIPTION: *Male*: Total length 1.00 (0.95–1.08). Carapace length 0.44 (0.43–0.47), width 0.40 (0.38–0.43), height 0.20 (0.19–0.23). Carapace with four setae (bases referred to as "tubercles" in Marusik et al., 2005) along midline and four laterally, two on each side (figs. 3, 4). Midline setae located on clypeus (one), slightly posterior to PME (one), and on dorsalmost carapace surface (two). Lateral setae located between LE (one pair), and slightly posterior to central one behind PME. Chelicerae with median keel ending in single strong promarginal tooth; retromarginal teeth absent (figs. 3, 5, 8, 9). Promargin of chelicera with three lateral short hairs with larger bases and rounded strong scale on dorsal surface (figs. 3, 6). Labrum globose, with minute denticles grouped on its ventral surface,

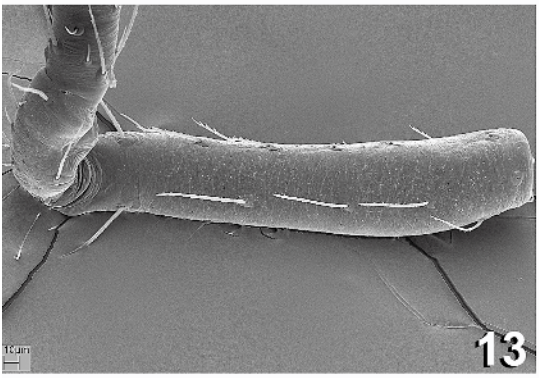


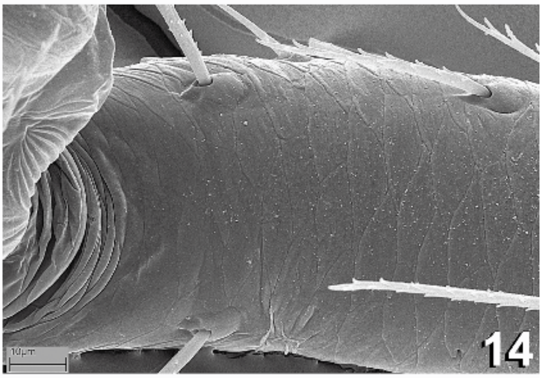
Figs. 7–10. *Synaphris saphrynis*, n.sp. Male paratype. **7.** Sternum, ventral view; **8.** Mouthparts, ventral view; **9.** Mouthparts, posterior view; **10.** Detail of mouthparts, showing labrum and labium, ventral view.

globose expansion arising from anterior surface (figs. 5, 8, 10). Maxillary setae scarce (figs. 5, 8, 10; compare to symphytognathid maxillary setae in Griswold et al. 1998: fig. 21C), distal maxillary setae clavate (arrow in fig. 5). Clypeus slightly convex, height 0.14 (0.12–0.15), ca. 5–6 AME diameters. Sternum length 0.27 (0.24–0.28), width 0.29 (0.26–0.30), length/width 0.96 (0.89–1.00), cuticle squamate (fig. 7), posterior margin truncated, wide, about two times width of coxa IV (figs. 2, 7). Abdomen oval, length 0.50 (0.47–0.64), width 0.44 (0.40–0.47), height 0.36 (0.36–0.43). Three epiandrous spigots centrally distributed along the epigastric furrow (figs. 31, 32). **Legs:** leg formula 4=123. Leg measurements: see table 1. Femoral spot and prolateral clasping spine absent (figs. 11, 13, 14). Setae on legs with large elevated, striated bases (figs. 17, 18, 20, 22). Leg tarsi without pseudosegmentation (figs. 12, 19, 23, 24). Tarsal-metatarsal joint constricted (figs. 11, 12, 16–18, 27). Distal area of metatarsi with dorsal band of anastomosed ridges (figs. 17, 18; the ‘‘subdistal anastomosed lyriform organ’’ of Marusik and Lehtinen, 2003). Legs without spines, tarsal organ located in middle dorsal region of tarsus, capsulate, with rounded orifice (figs. 19, 20). Three claws, serrate accessory (false claw) setae present. Claw teeth (paired claws/ inferior claw): Leg **I**, paired claws with five teeth/ inferior claw with two teeth and one dorsal denticles (figs. 23–25); **II** and **III**, four teeth/ as leg I; **IV**, two teeth/ two teeth and one dorsal denticle (figs. 28, arrow in 29). Distal tooth two times longer than other teeth in paired claws. Leg hairs serrate. Cuticular surface of appendages squamate (fig. 20). Tarsus slightly longer than metatarsus on legs I and II, same length on legs III and IV (see table 1, figs. 11, 12, 16, 27). **Trichobothria:** Trichobothrial bases simple and smooth, with proximal hood bearing two lateral ridges, similar on all legs and segments (figs. 15, 21, 22). Tarsal trichobothria absent. Legs **I** and **II**, tibia 1-1-0;

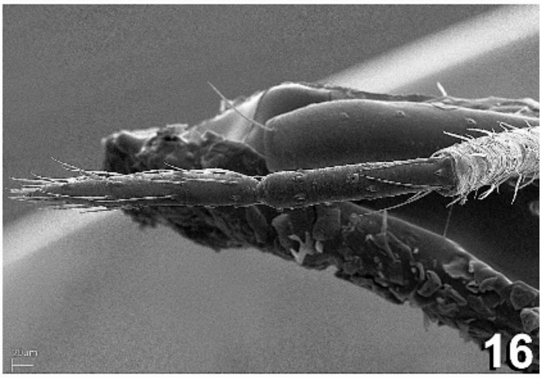

20µm
11

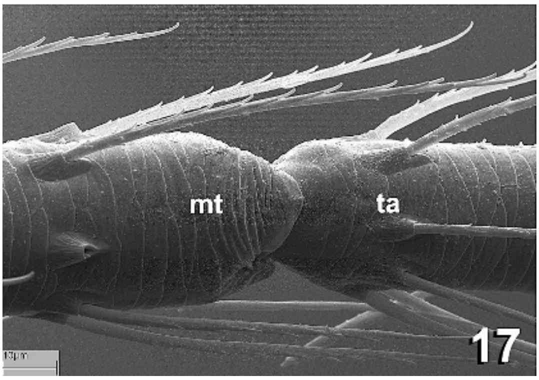

10µm
12

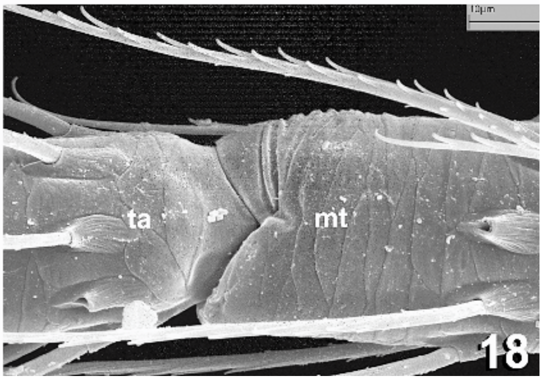

10µm
13


10µm
14


20µm
15


20µm
16


mt
ta
10µm
17


10µm
ta
mt
18

metatarsus 0-1-0. Legs **III** and **IV**, tibia p1-2-0-0; metatarsal trichobothria absent. **Color:** Carapace brown with undefined lighter radii, surface slightly wrinkled; sternum brown, darker than carapace, not homogeneous but without definite pattern, border with thick orange stripe. Legs orange. Abdomen greenish black, with pattern of irregular transversal lighter bands. **Eyes:** AME black, other eyes pearly white. Diameter: AME 0.02, PME 0.02, PLE 0.03, ALE 0.04. **Respiratory system:** Anterior booklungs transformed into tracheae, connected by a transverse duct (figs. 30, 35–37, 39). Anterior spiracles connected to epigastric furrow (figs. 2, 31). Five tracheal tubes arise from each anterior spiracle, four oriented anteriorly toward cephalothorax, one oriented laterally first, then turning posteriorly. Posterior tracheal system (figs. 30, 34, 37–39) with two distant spiracular openings (figs. 2, 33) exteriorly connected by thin ridge (i.e., one wide spiracular opening). Thin ridge leading to deep, flat, membranous atrium, anteriorly ending in sclerotized U-shaped duct that connects tracheal ducts arising from spiracles. Two main tracheal bundles arise from the junction of tracheal ducts and U-shaped atrial duct, one on each side, directing tracheoles mainly anteriorly. Smaller clumps diverge laterally, some tracheoles seem to branch off clumps and disperse irregularly around abdominal space. Both tracheal systems seem to reach into prosoma. **Spinnerets** (fig. 40): Colulus large and fleshy, triangular, about half length and width of ALS, with three setae (fig. 41). ALS (fig. 42) with one MAP spigot, accompanied by nubbin and tartipore, separated by weak furrow from PI field, which contains four piriform spigots with reduced bases, interspersed with few tartipores. PMS (fig. 43) with only one spigot, no nubbin. PLS (figs. 44, 45) with only two spigots of different morphology (see Discussion below). **Palp** (figs. 46–62): Tibia rounded retrolaterally, without apophyses (figs. 47, 53, 55). One tibial trichobothrium located dorsal and distally (fig. 56). Cymbium capsulated, comprising two distinct areas: one rounded, dorsal, retrolateral, with hairs, one membranous (indistinguishable under light microscope), prolateral, with no setae (figs. 49, 54). Retrolateral margin of cymbium with notch delimiting basal paracymbium (figs. 47, 52, 53, 60). Measurements: femur 0.12 (0.11–0.14), patella 0.05 (0.05–0.06), tibia length 0.07(0.06–0.07), tibia width 0.12 (0.09–0.12), tibia length/width 0.55 (0.55–0.67). Embolus filiform, long, thin with thickened tip (figs. 46, 51, 59, 62). Embolar base flat, ventral, with dorsal flat translucent, membranous expansion (figs. 46, 49, 50; "lamella", Marusik et al., 2005; Marusik and Lehtinen, 2003). Base of embolar expansion about 2/5 its maximum width. Embolus running clockwise (in left palp), exteriorly surrounding junction of two areas of cymbium, which areas may act as cymbial conductor (figs. 46, 54). Tegular groove also present, accompanying embolus toward tip of bulb, terminating in pointed apophysis (figs. 50, 59; "terminal apophysis", Marusik et al., 2005; Marusik and Lehtinen, 2003). This apophysis may act as conductor, and presents small pore opening close to tip (fig. 61).Dorsal edge of embolar expansion with weak furrow, which might also be related to embolus (figs. 50, 51). Ventral to pointed apophysis is another apophysis, with two pointed tips (figs. 50, 57, 58; "subterminal apophysis", Marusik et al., 2005; Marusik and Lehtinen, 2003). Spermatic duct seems to undergo one transverse loop before reaching embolar base. Diameter of spermatic duct gradually decreases throughout its length, except for a sudden widening before entering base of embolus for fraction of loop length (arrow in fig. 48).

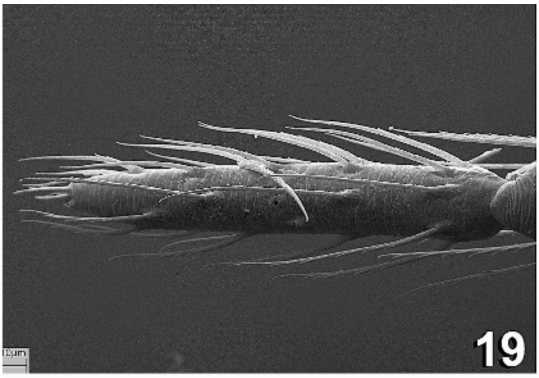
Female: Unknown.

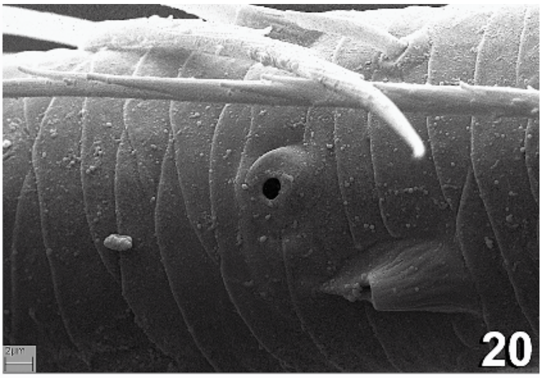
NATURAL HISTORY: The specimens were collected in pitfall traps from dry wheat and barley fields.

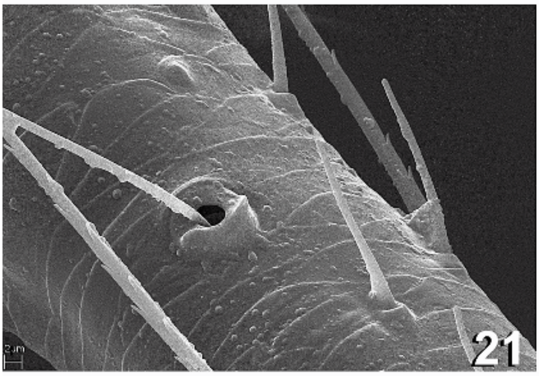
DISTRIBUTION: Known only from the type locality.

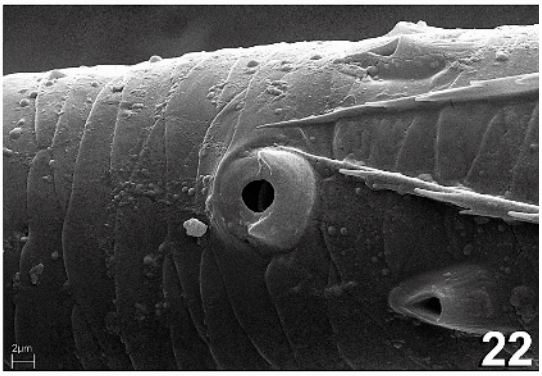
←

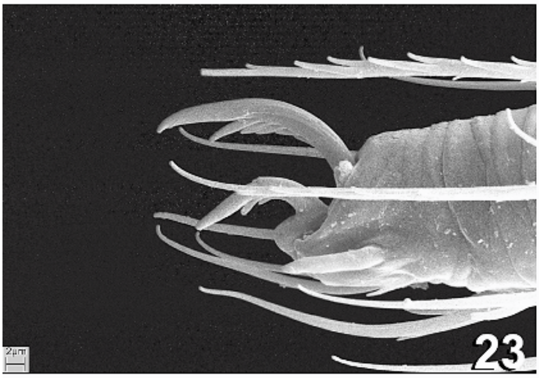
Figs. 11–18. *Synaphris saphrynis*, n.sp. Male paratype, right leg I. **11.** Prolateral view; **12.** Tarsus and metatarsus, retrolateral view; **13.** Femur, ventral view; **14.** Same, detail at femoral spot area; **15.** Tibia and patella, dorsal view; **16.** Tarsus and metatarsus, dorsal view; **17.** Detail of tarsus-metatarsus joint, dorsal view; **18.** Same, prolateral view.

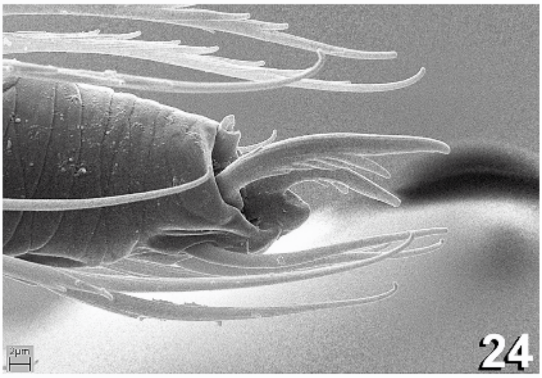

10µm
19

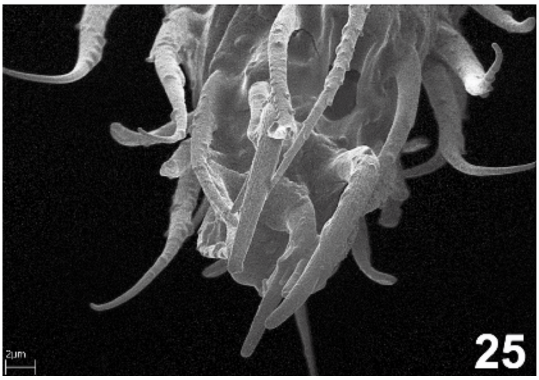

2µm
20

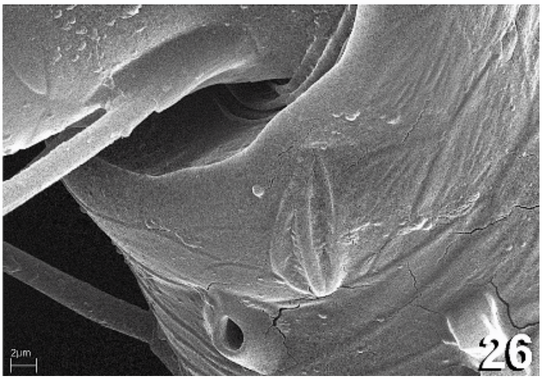

2µm
21

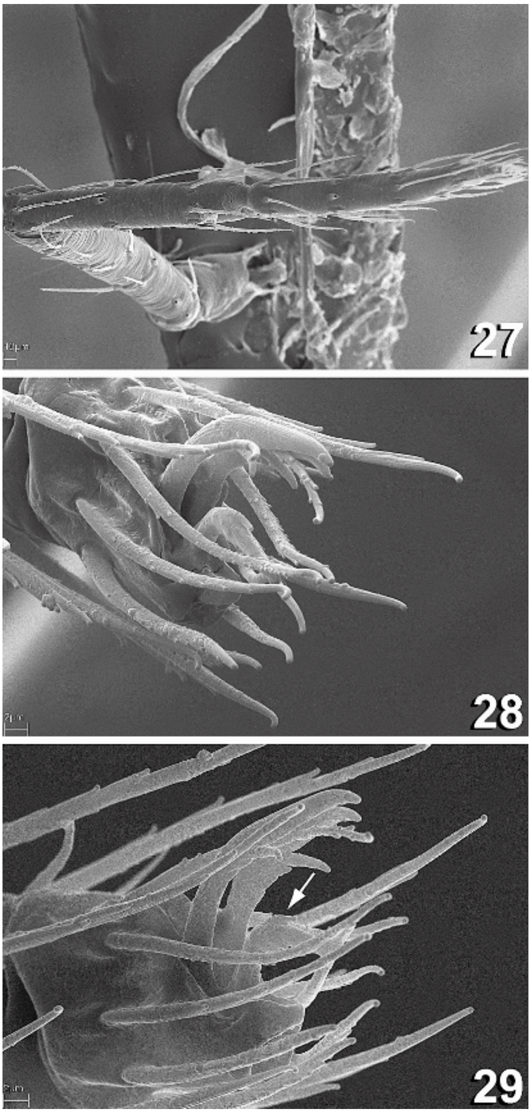

2µm
22


2µm
23


2µm
24


2µm
25


2µm
26



Figs. 27–29. *Synaphris saphrynis*, n.sp. Male paratype, right leg IV. **27.** Tarsus and metatarsus, dorsal view; **28.** Tarsal claws, frontal-retrolateral view; **29.** Same, retrolateral view, arrow to dorsal denticle on inferior claw.

Other Material Examined: SPAIN: **Toledo:** Huecas, same locality, 29.v.2003, 6 ♂; 15.v.2003, 1 ♂, Kleijn et al. col. (A. Melic 5739-A).

Cepheia longiseta (Simon, 1894)
figures 63–80

Description of Spigot Morphology: *Male*: Colulus large, fleshy, triangular, about half length and width of ALS, with three setae (figs. 63, 64). ALS (figs. 65, 66) with one MAP spigot, accompanied by a nubbin and a tartipore, separated by weak (almost nonexistent) furrow from PI field. PI field, on external side of ALS, contains three PI spigots with reduced bases, posterior PI spigot base larger. PMS (figs. 67, 68) with two spigots of similar morphology, chemosensory seta (can be confused with spigot) located anteriorly; externally, its base deepens around shaft. PLS (figs. 69–71) with two spigots of slightly different morphology clumped in same field. Internal one with rounded, larger base and more cylindrical shaft, external one with oval base and tapering shaft. Short, thick chemosensory seta (can be confused with a small spigot) located more basally on internal side of distal PLS segment.

Female: Colulus large, fleshy, triangular, about half length and width of ALS, with four setae (figs. 72, 73). Spinnerets as in male, except: four PI spigots (instead of three) on ALS (figs. 74, 75); one external CY spigot on PMS (figs. 76–78); and one internal CY on PLS (figs. 79, 80).

Material Examined: 1♂ and 1♀ paralectotypes from FRANCE ("Gallia") coll. Simon 4538, b.849 (MNHN-AR 1059).

Distribution: *Cepheia longiseta* has been collected from dry regions and coastal areas of the western Mediterranean region in southern

---

←

Figs. 19–26. *Synaphris saphrynis*, n.sp. Male paratype, right leg I. **19.** Tarsus, dorsal view; **20.** Same, detail of tarsal organ; **21.** Tibia, dorsal view, detail of trichobothrial base; **22.** Metatarsus, dorsal view, detail of trichobothrial base; **23.** Tarsal claws, prolateral view (prolateral superior claw broken); **24.** Same, retrolateral view; **25.** Same, dorsal view; **26.** Tibia-metatarsus joint, prolateral view.

30

Fig. 30. *Synaphris saphrynis*, n.sp. Male paratype, schematic drawing showing tracheal system, dorsal view.

France (Simon, 1881, 1894, 1926; Denis, 1933a,b; Brignoli, 1970), northern Italy (Bertkau, 1890; Thaler and Noflatscher, 1990), southern Spain (Wunderlich, 1980; Thaler and Noflatscher, 1990), and southern Austria (Thaler, 1993). John Murphy (personal commun.) has collected *C. longiseta* in the southern part of the Iberian Peninsula (Portugal: Algarve Province, Faro; Spain: Almeria and Malaga Provinces) and the Baleares Islands (see fig. 1).

DISCUSSION

Spinneret Morphology and Webs in Synaphridae

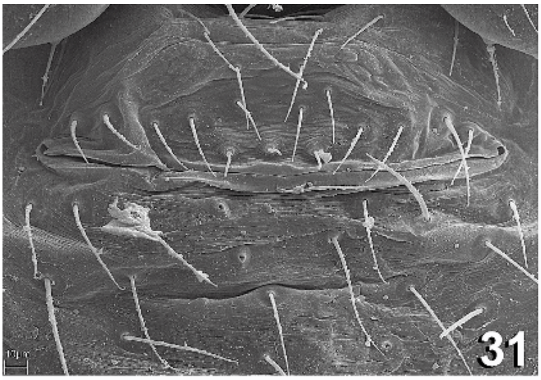
Males and females of *C. longiseta* and *S. saphrynis* present one major ampullate spigot on their ALS that is separated from the piriform field by a weak furrow, and it is accompanied by a nubbin and a tartipore. In *C. longiseta*, the PI field presents few piriform spigots, the posterior one with enlarged and more distinctive base. Piriform spigots with different size bases seem to also occur in other spiders (Martín J. Ramírez, personal commun.).

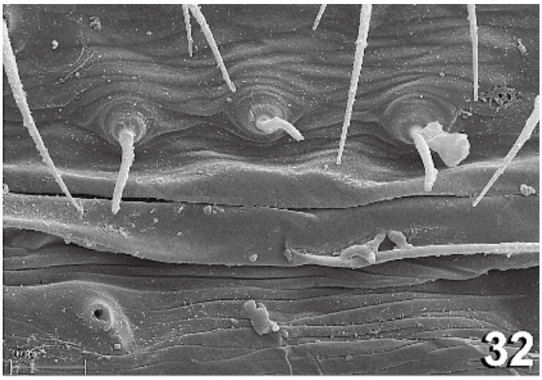
The presence of only one spigot on the PMS of *S. saphrynis* and two morphologically similar PMS spigots in *C. longiseta* (not including the cylindrical spigot in females) suggest that these spigots are either minor ampullate silk gland or aciniform silk gland spigots, although these spigots do not necessarily serve the same silk glands in each species. A single spigot is also present in the two recently described *Synaphris* species and the new synaphrid genus from Madagascar, which has been assigned to a minor ampullate gland (Miller, in press), in which case it would be homologized to that of *S. saphrynis* as well. Unfortunately, external morphology alone is not sufficient to discriminate between these two spigot types. In the case of *C. longiseta*, the two PMS spigots most likely correspond to aciniform gland spigots, as the presence of two minor ampullate spigots in araneoid adults is rare. Also, the anterior chemosensory seta in the PMS of *C. longiseta* has been previously considered a median-anterior minor ampullate silk gland spigot (Schütt, 2003), although its morphology is similar to the chemosensory seta on the female palp tip (see Lopardo and Hormiga, in press, fig. 12).

The PLS in both *S. saphrynis* and *C. longiseta* have two types of spigots in addition to the cylindrical spigot found only in females. If one of these two is an aciniform spigot, at least one spigot from the araneoid triad would have been retained. Consequently, the PLS retained the combination of either one aciniform plus one triad spigot (flagelliform or aggregate), or one aggregate plus flagelliform (a ‘‘triplet’’ of two spigots) and no aciniform. As is the case of the singular PMS spigot in *Synaphris*, external morphology alone is not sufficient to discriminate between these two spigot types.

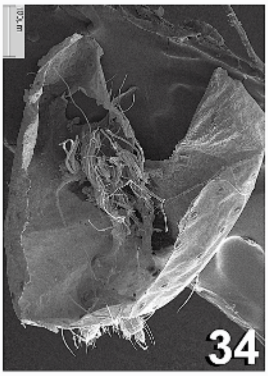
The weak demarcation of the major ampullate field from the piriform field on the ALS of *Synaphris saphrynis* and *Cepheia longiseta* (coded as absent in *Cepheia* by Schütt, 2003; see also Miller, in press) contradicts the evidence supporting Synaphridae as a member of Araneoidea. Should the monophyly of Synaphridae and its current placement within Araneoidea hold, then Synaphridae would become the only araneoid family with a weakly demarcated major ampullate field (as proposed by Schütt, 2003), a condition that is common outside Araneoidea (Griswold et al., 2005). Based on the morphology of PLS spigots, we could describe synaphrid spiders as having retained at least one of the three triad spigots on their PLS in both sexes.

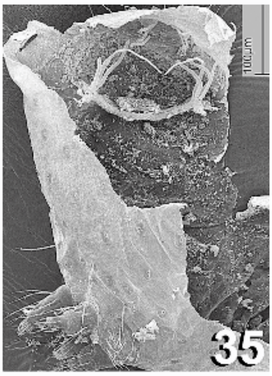
The web of only one species of synaphrids has been reported. *Synaphris lehtineni* builds a small, thin sheet web underneath stones in hollow depressions where they live (Marusik et al., 2005: 129). The web building behavior of *S. lehtineni* and the rest of synaphrid species is still unknown. The presence of only one AG and one FL spigot on the PLS has also been reported for the linyphiid *Linyphia hortensis* (Schütt, 1995), which spins a small sheet web composed in part by sticky silk (at least for juveniles, Benjamin and Zschokke, 2004), although the details of the sticky thread structure have not been studied. Given that one of the alternative interpretations of the PLS spigot composition in synaphrids is the retention of a triplet consisting of one AG and one FL spigot, then it is possible that these spiders also spin webs that include some kind of sticky silk.

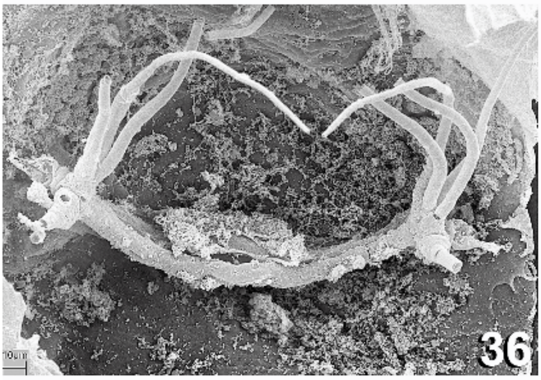

10µm
31

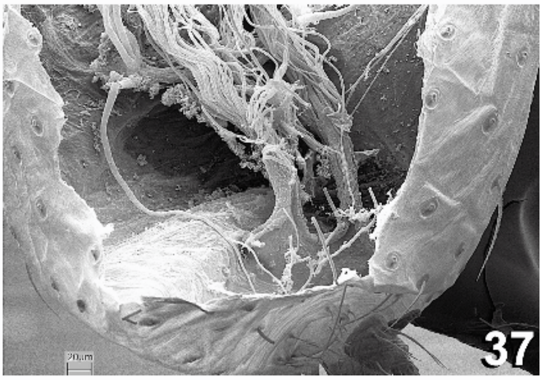

32

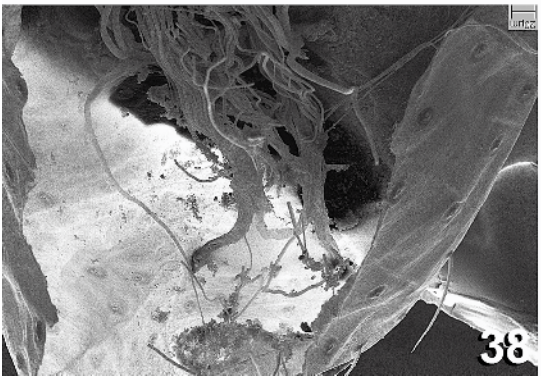

10µm
33

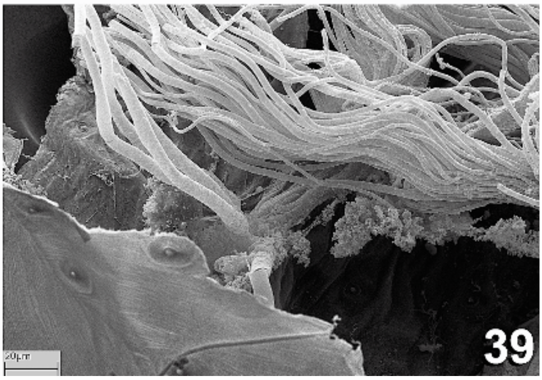

100µm
34

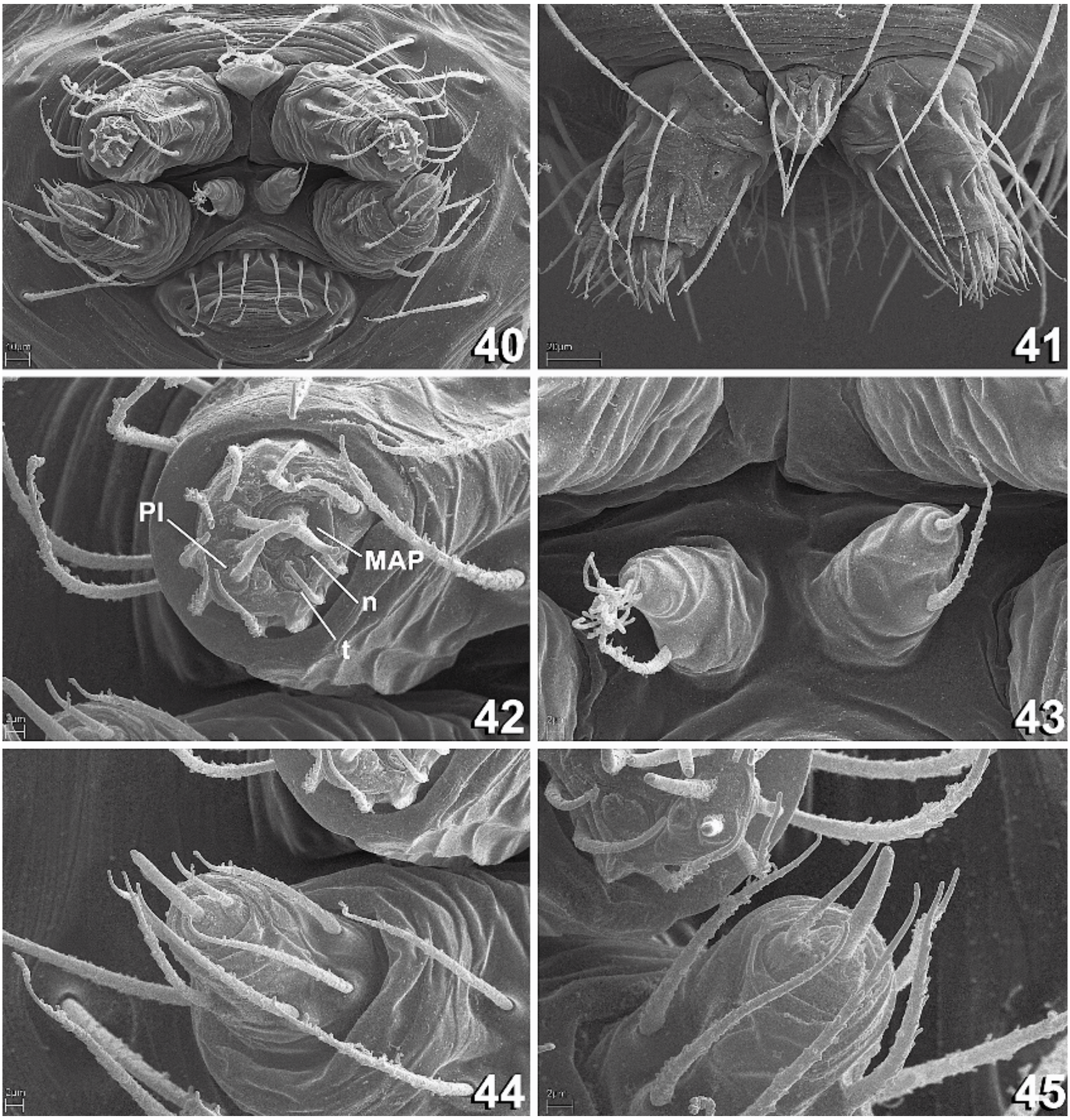

100µm
35


10µm
36


20µm
37


38

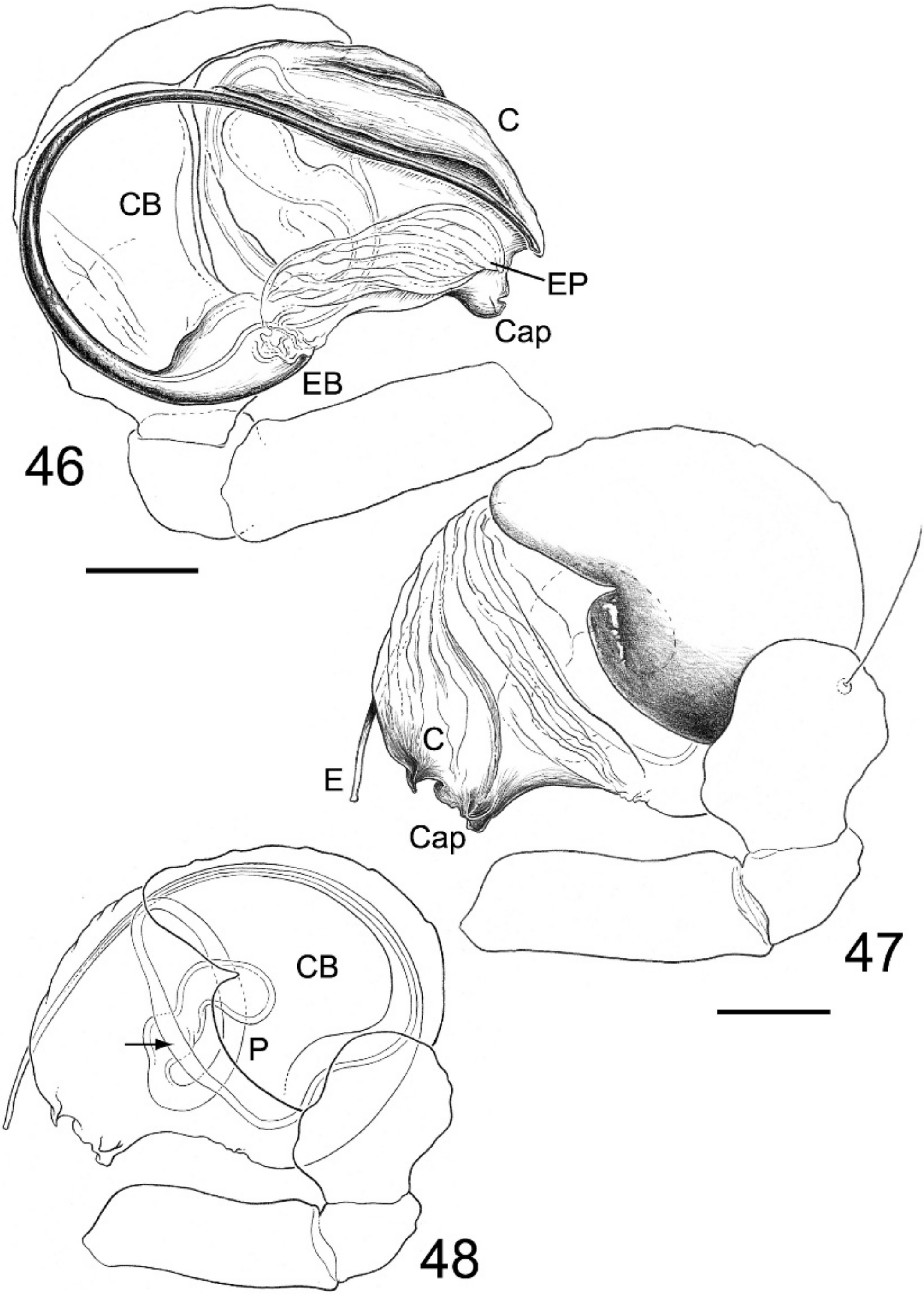

20µm
39



Figs. 40–45. *Synaphris saphrynis*, n.sp. Male paratype, spinnerets. **40.** Spinning field; **41.** Same, ventral view; **42.** Right anterior lateral spinneret; **43.** Posterior median spinnerets; **44.** Right posterior lateral spinneret; **45.** Left posterior lateral spinneret. Abbreviations are spelled out in appendix 1.

←

Figs. 31–39. *Synaphris saphrynis*, n.sp. Male paratype, respiratory system and epiandrous spigots. **31.** Anterior respiratory spiracles and epigastric furrow; **32.** Same, detail of epiandrous spigots; **33.** Posterior respiratory spiracles; **34–39:** Digested abdomen showing internal tracheal arrangement; **34.** Anterior and posterior tracheae, general view; **35.** Anterior tracheae, general view; **36.** Same, detail on anterior tracheal arrangement; **37.** Detail of posterior tracheae; **38.** Same; **39.** Same, showing both tracheal arrangement.



Figs. 46–48. *Synaphris saphrynis*, n.sp. Male paratype, left palp. **46.** Prolateral view; **47.** Retrolateral view; **48.** same, cleared. Abbreviations are spelled out in appendix 1.

THE POSITION OF *SYNAPHRIS SAPHRYNIS* n.sp. WITHIN *SYNAPHRIS*

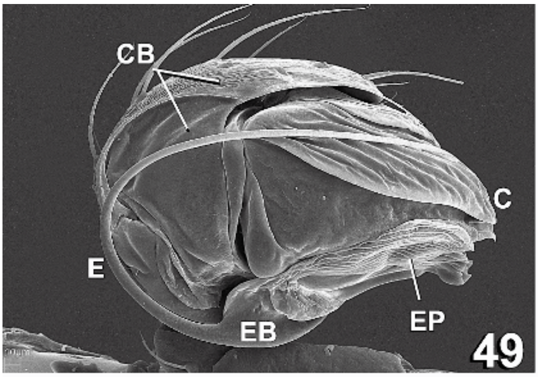
Marusik and Lehtinen (2003: 150) divided *Synaphris* into two separate species groups, although they did not provide an explicit phylogenetic justification for the monophyly of these two groups. Although the diagnostic characters for these two species groups seem sound, the monophyly of the two groups remains untested, and species membership to the species groups seems to be based on overall similarity. The *letourneuxi* group includes those species with palpal embolic lamella, two distal apophyses (the ventral one bipartite), a tegular groove accompanying the distal portion of the embolus, coiled copulatory ducts in females, and the absence of an epigynal depression. Species of this group are distributed from the Mediterranean region to Central Asia. The *calerensis* group includes those species without embolic lamella (although, as these authors suggested, this feature should be carefully checked), two entire distal apophyses, no tegular groove, and an oval depression in the epigynal area. Species of this group are endemic to the Canary Islands. The presence of an embolic lamella, a lower apophysis bipartite, and the tegular furrow in *Synaphris saphrynis*, n.sp. suggest that this species belongs to the *letourneuxi* group.

PALPAL MORPHOLOGY OF *SYNAPHRIS*

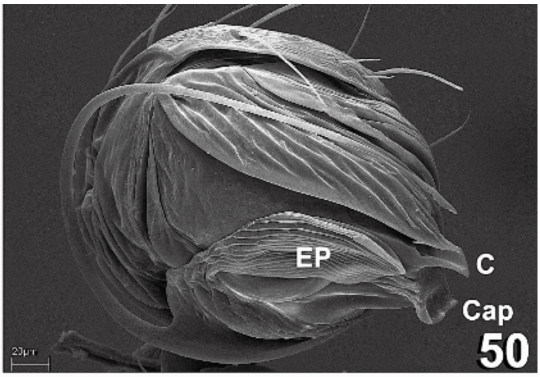
The palpal morphology of *Synaphris saphrynis*, n.sp. is very similar to that of *S. letourneuxi* (Simon, 1884), the type species; therefore, its generic placement is rather straightforward, although it has not been phylogenetically tested. The male palp of *Synaphris* is characterized by a cymbium divided into two separate areas: a sclerotized one bearing setae and a glabrous, membranous one, the latter one on the prolateral side. The retrolateral margin of the cymbium in *Synaphris* presents a notch delimitating a basal expansion, with cuticular differentiation, which most certainly is a paracymbium (fig. 60; Marusik and Lehtinen, 2003; Miller, in press).

The embolus base is extended into a membranous "lamella", and the tegulum is flat and oval. Homology statements regarding palpal sclerites and apophyses are notoriously difficult to test (e.g., Griswold et al., 1998; Hormiga and Scharff, 2005), sometimes even at the primary stage of the homology proposition. The tegulum of *Synaphris saphrynis* is distally extended into a large and less sclerotized area, which bears several apophyses and a longitudinal fold that houses the distal region of the embolus (figs. 50, 59). There are no clearly delimited or membranous attached tegular sclerites (such as those often found on the tegulum of many araneoids), except for the embolus and the membrane that arises from the membranous stalk that connects the tegulum to the embolus base (the so-called embolic "lamella").

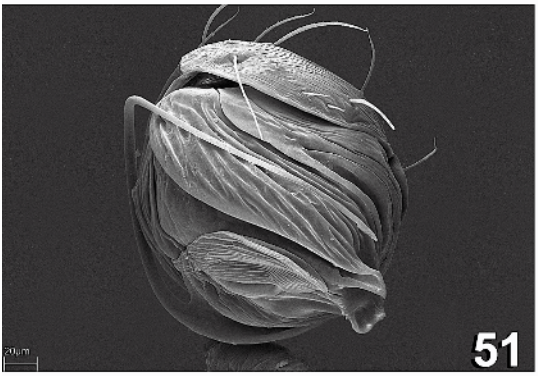
In their detailed description of the male palpal morphology of *Synaphris lehtineni* (Marusik et al., 2005) and *S. orientalis* (Marusik and Lehtinen, 2003), the authors use a rich terminology to name and label the various tegular processes (the palpal morphology of these two species is very similar to that of *S. saphrynis*, n.sp.). Some of the anatomical terms used by Marusik and coworkers have a long history in palpal morphology (e.g., "terminal apophysis"). Although the choice of names of these morphological features implies homology to at least some of the equally named sclerites in other taxa, these authors do not discuss the potential correspondence of the palpal sclerites of *Synaphris* with those of other araneoid taxa. Interestingly, Marusik et al. (2005) did not label any of the tegular sclerites as a "conductor", but mentioned that the terminal part of the embolus lies in a "tegular groove" and that such tegular groove would be unique (autapomorphic) within Araneoidea. These authors also provided names for the tegular processes: "subterminal apophysis" (the one at the end of the conductor) and "terminal apophysis" ("Cap", or conductor apophysis). Both names have been used by other araneologists for sclerites in araneoid taxa. We propose what is perhaps a simpler alternative, namely that the distally extended tegular area of *Synaphris* is a homolog of the araneoid conductor and that the "subterminal" and "terminal" apophyses of Marusik et al. are processes of the conductor. As is often the case, this conductor partly



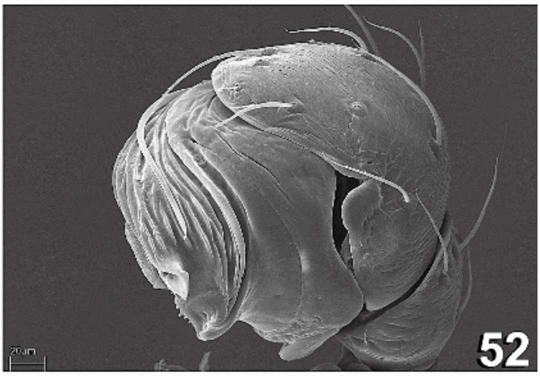
49



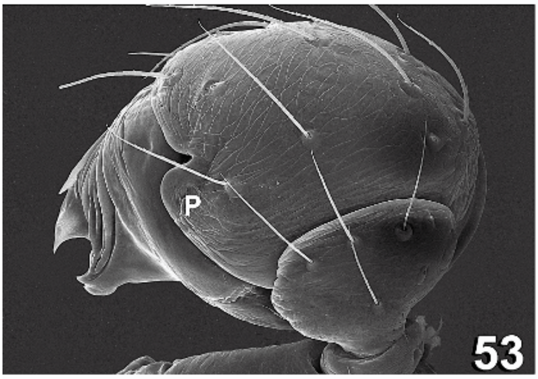
50



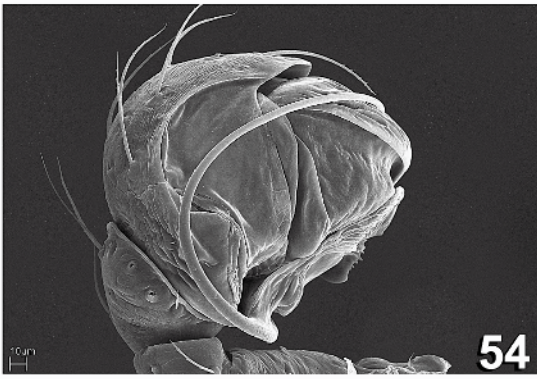
51



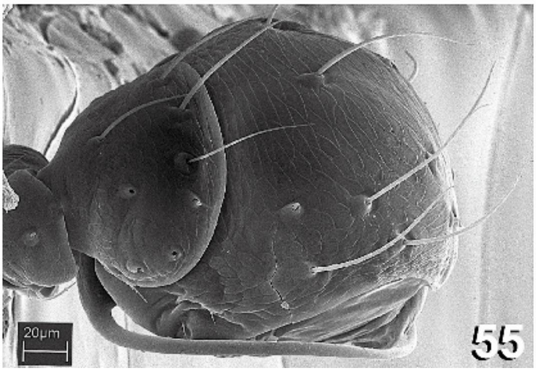
52



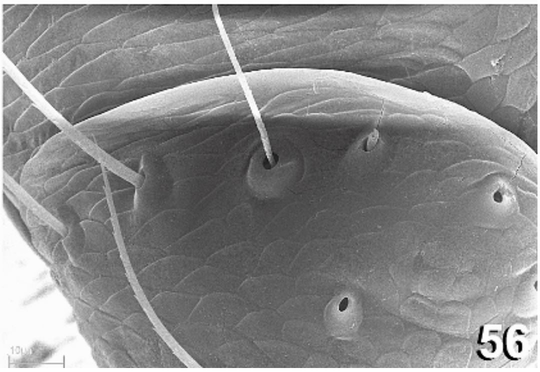
53



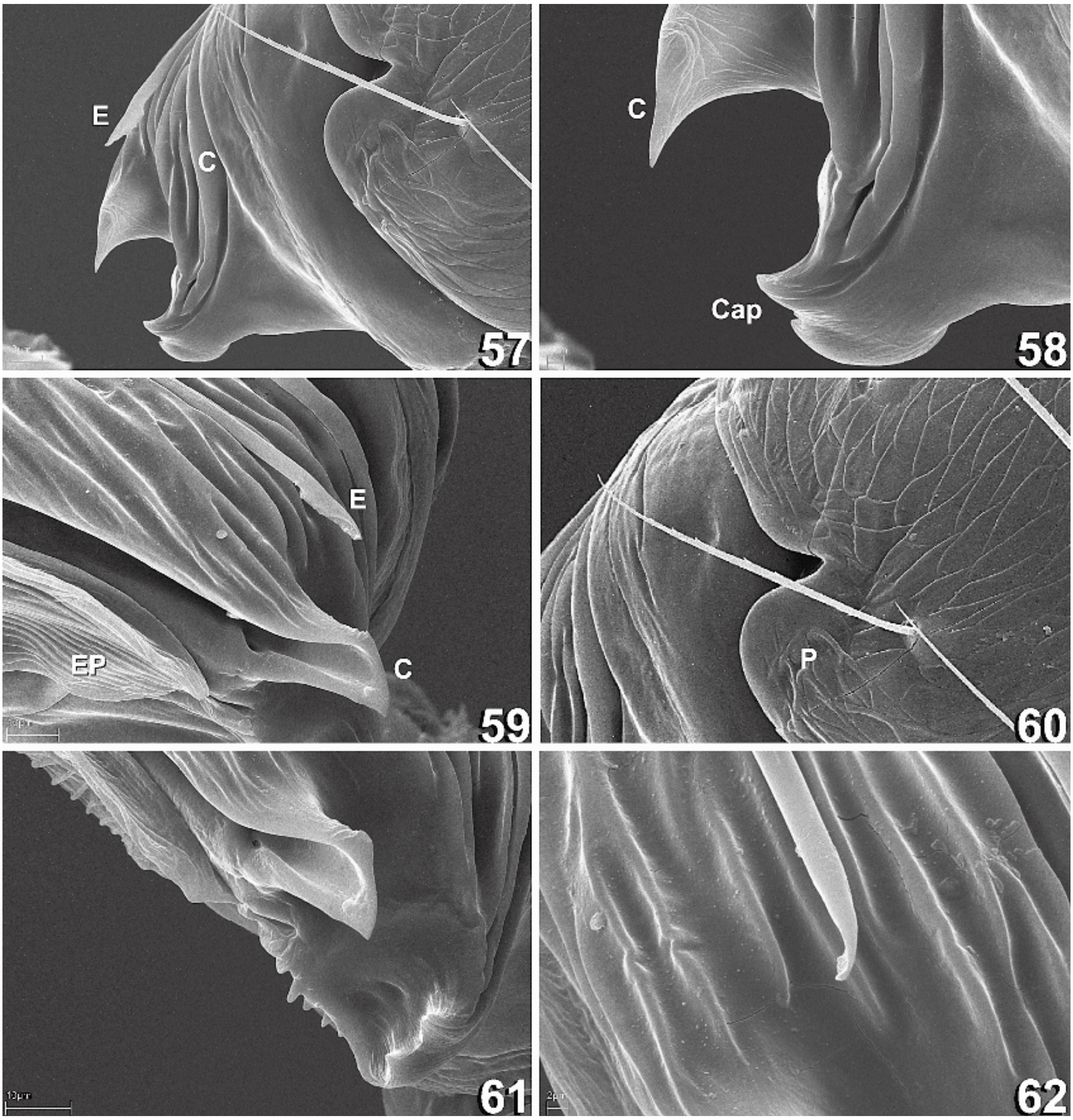
54



55



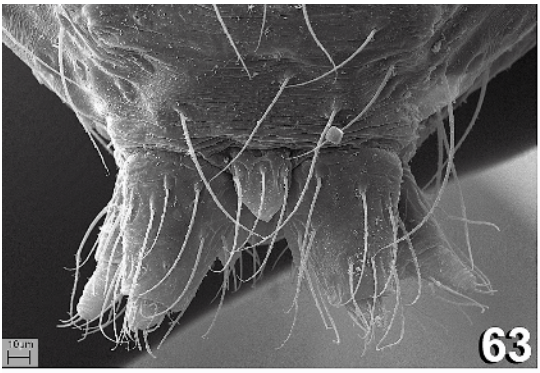
56

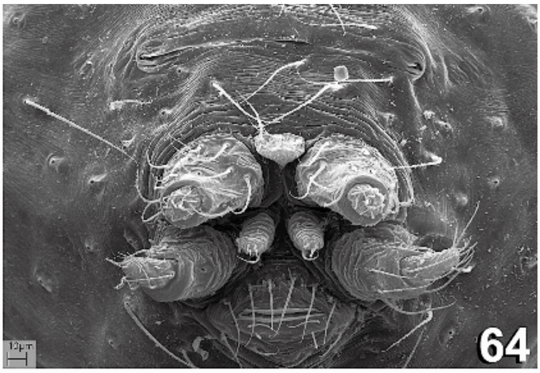


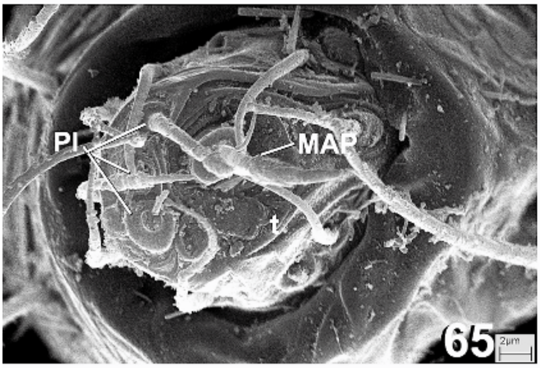
Figs. 57–62. *Synaphris saphrynis*, n.sp. Male paratype, left palp, details. **57.** Detail of apex, showing embolus, terminal and subterminal apophyses, and paracymbium, in retrolateral view (detail of fig. 53); **58.** Same, closer view of terminal and subterminal apophyses; **59.** Detail of apex in apical view (detail of fig. 51); **60.** Detail of retrolateral paracymbium; **61.** Detail of apophyses, apical view; **62.** Embolus tip. Abbreviations are spelled out in appendix 1.

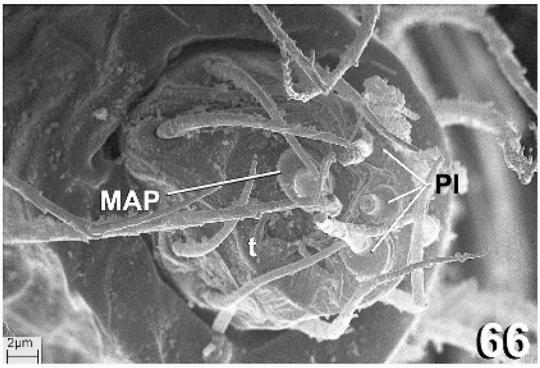
←

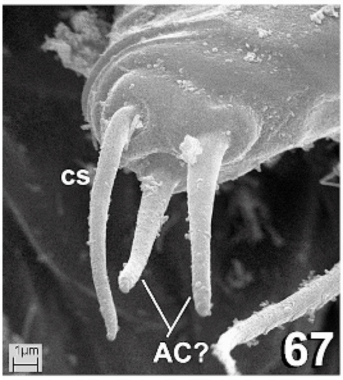
Figs. 49–56. *Synaphris saphrynis*, n.sp. Male paratype, left palp. **49.** Prolateral view; **50.** Prolatero-apical view; **51.** Apical view (see detail in fig. 59); **52.** Apical-retrolateral view (see detail in fig. 62); **53.** Retrolateral view (see detail in figs. 57, 60); **54.** Dorso-prolateral view; **55.** Dorsal view; **56.** Detail of palpal tibia and tibial trichobothrial base. Abbreviations are spelled out in appendix 1.

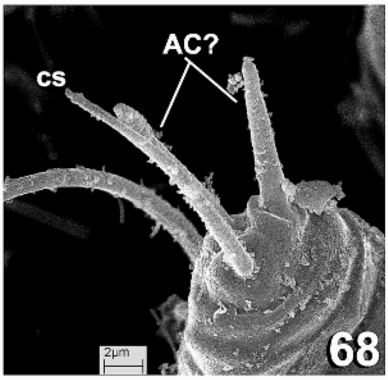

10µm
63

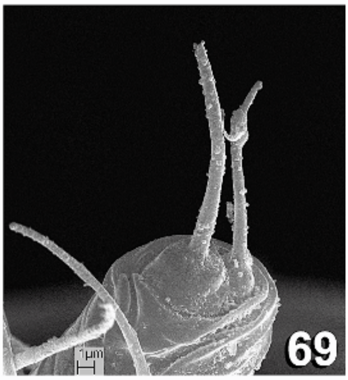

10µm
64

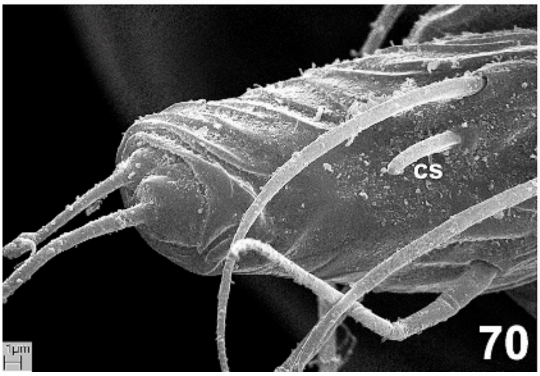

PI
MAP
t
65
2µm


MAP
PI
t
2µm
66


cs
AC?
1µm
67


AC?
cs
2µm
68


1µm
69


cs
1µm
70


cs
2µm
71

covers (in a groove or fold in this particular case) the distal region of the embolus. The presence of processes or apophyses on the conductor has been documented in other araneoid taxa (e.g., in Synotaxidae and Anapidae; see for example Platnick and Forster, 1989: fig. 55). The palp of *S. saphrynis*, n.sp. also exhibits these two separate sclerotized and distinct conductor apophyses.

SYNAPOMORPHIES FOR SYNAPHRIDAE

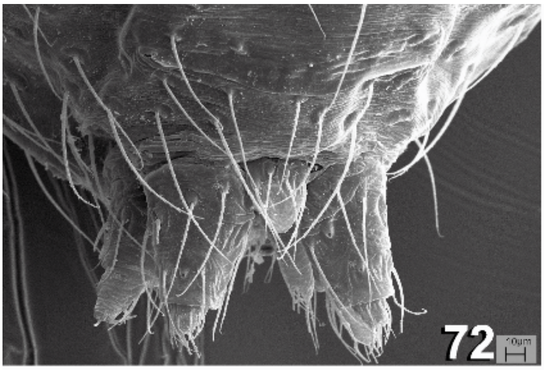
Of a total of 12 described species in Synaphridae, 7 of them (five *Synaphris* species, *Cepheia longiseta* and a new Malagasy genus) have been studied using scanning electron microscopy (this study; Marusik and Lehtinen, 2003; Marusik et al., 2005; Miller, in press; Lopardo and Hormiga, in press). Based on study of two *Synaphris* species, Marusik and coworkers have proposed family-level synapomorphies. Those include anastomosing lyriform organs on subdistal metatarsi; a cheliceral keel that ends in a single strong prolateral tooth (or "tooth-like projection", Schütt, 2003; also "process with pointed tip", Marusik and Lehtinen, 2003); a flattened and transparent extension of the embolic base called "lamella"; palpal tibia pressed against the cymbial base and with two pits (Marusik and Lehtinen, 2003: 147, fig. 17); embolar and cymbial conductor; a notched tibial trichobothrial base; pseudosegmentation of tarsi (Marusik et al., 2005); and tarsi longer than metatarsi. These synapomorphies are discussed below, and new synapomorphies are proposed.

Metatarsal subdistal anastomosed lyriform organs (Marusik and Lehtinen, 2003: 147, 150). This special lyriform organ has not been clearly defined nor properly documented and illustrated. A similar organ is present in *S. saphrynis*, n.sp. (figs. 17, 18), as a dorsal band of anastomosed ridges (compare it to the lyriform organ on tibia-metatarsus joint in fig. 26). This organ is also present in other symphytognathoids such as anapids and mysmenids (LL and GH, personal obs.) and seems to also be present in theridiids (e.g., Agnarsson, 2004: fig. 84E; also Jeremy Miller, unpubl. data), theridiosomatids and even in uloborids (Jeremy Miller, unpubl. data). In light of the mentioned evidence this organ can no longer be accurately described as "a pattern that is not known in other higher Araneoidea" (Marusik and Lehtinen, 2003: 147). Furthermore, the presence of this organ in Uloboridae suggest that is it widespread at least within Orbiculariae, although might be present in other non-orbicularian spiders as well. In this paper we illustrate this organ for the family, for future reference. Nevertheless, a putative synapomorphy for the family seems to be the **constriction on the tarsi-metatarsi joint** on every leg and both sexes, which we do not know for any other Araneoidea, except for the pimoid genus *Nanoa* Hormiga, Buckle and Scharff 2005 (Hormiga et al., 2005: 252; GH, personal obs.).

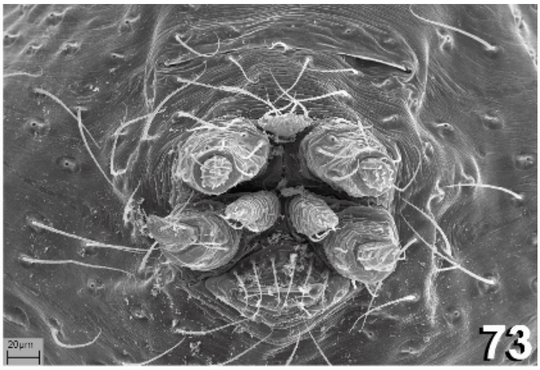
The presence of a **cheliceral keel that ends in a strong promarginal cheliceral tooth** seems to also define the family (Wunderlich, 1986, 1995; Schütt, 2003), although it is not unique to Synaphridae. The concept of "cheliceral keel" has been previously used to name different structures. The following discussion stems from the premise that anatomical terminology should reflect hypotheses of homology. This cheliceral structure has been correctly defined as "the inner side of the paturon showing a distinct edge over the entire length" by Schütt (2003: 141), but it has also been defined as a "serrated ridge, truncated outgrowth of the cheliceral *distal* margin" (Ubick et al., 2005: 266, fig. 72.41; our italics). Alternatively, the cheliceral keel (as defined by Schütt, 2003) has been referred as a "process with pointed tip" by Marusik and Lehtinen (2003), but also as a cheliceral "lamina" for the Tetrablemmidae by Lehtinen (1981). Furthermore, the term "lamina" has been equated to the cheliceral "lamella",

←

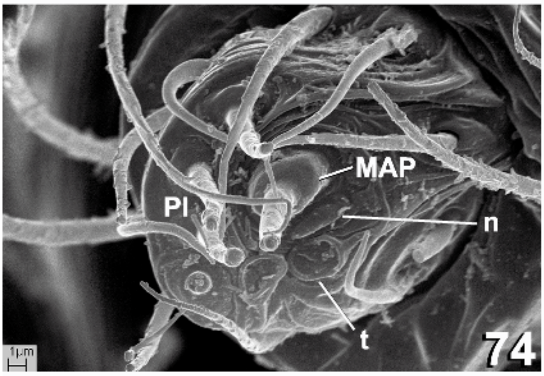
Figs. 63–71. *Cepheia longiseta*. Male paralectotype, spinnerets. **63.** Spinning field, ventral view; **64.** Same, posterior view; **65.** Right anterior lateral spinneret; **66.** Left anterior lateral spinneret; **67.** Right posterior median spinneret; **68.** Left posterior median spinneret; **69–71.** Right posterior lateral spinneret. Abbreviations are spelled out in appendix 1.



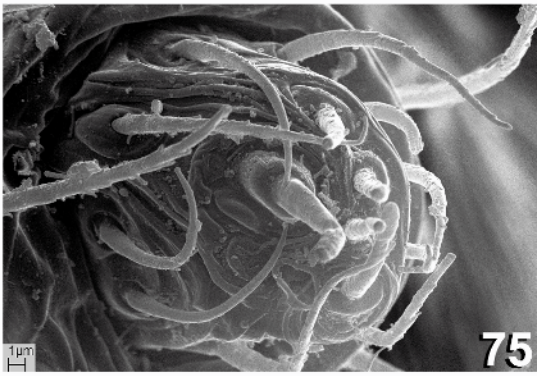
72



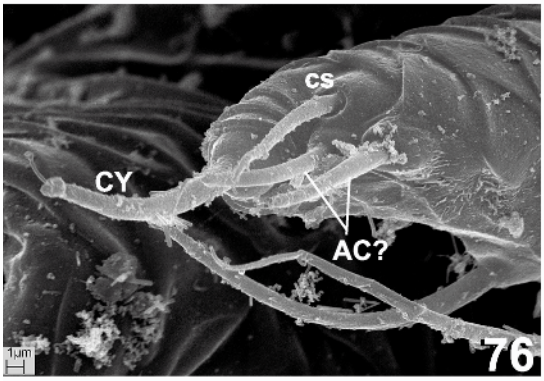
73



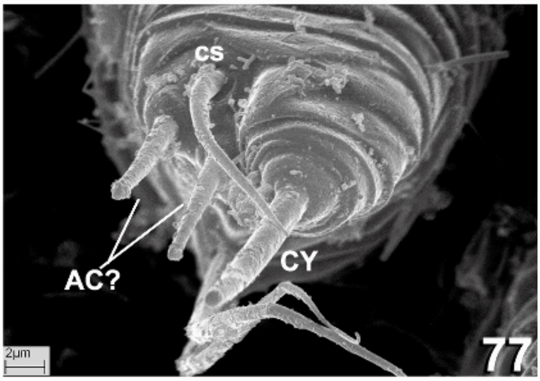
74



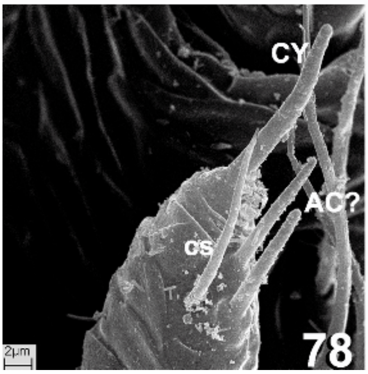
75



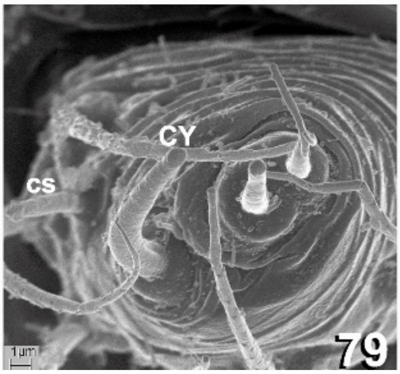
76



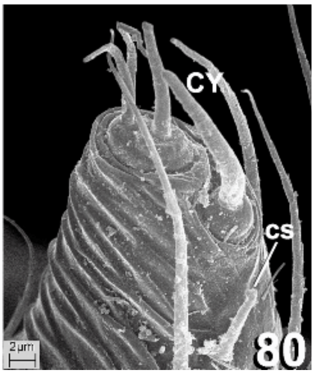
77



78



79



80

defined as a "sclerotized ridge on the cheliceral margin or mesal surface" (i.e., Schütt's keel; Ubick et al., 2005: 266, fig. 72.40). So far, the terms "keel" (sensu Schütt, 2003), "lamina", and "cheliceral lamella" would appear to be comparable, except that the "cheliceral lamella" has been previously defined as a different structure. Kaston (1978: 269) defined the cheliceral lamella as "a triangular plate on the promargin of the cheliceral fang furrow in some spiders, resembling a broad tooth, and forms a kind of chela with the fang". Moreover, the term (cheliceral) "lamella" sensu Kaston (1978) has been widely used in descriptions of haplogyne spiders, although under the name of "lamina" (e.g., Platnick et al., 1991; in the Gnaphosidae, Platnick, 1975; Medan, 2001; and in the Zodariidae, Szüts and Jocqué, 2001). Because the confusing term cheliceral "lamina" has been used to refer to either the cheliceral "lamella" or the cheliceral "keel", we think that, given the misunderstanding, the term lamina should be avoided whenever possible, and replaced by its respective synonyms. The cheliceral "keel" should be defined as a distinct sclerotized ridge on the inner side of the paturon over its entire length. The term cheliceral "lamella" has been clearly defined by Kaston (1978). Regarding the "other keel" (the "serrated ridge, truncated outgrowth of the cheliceral *distal* margin" [Ubick et al., 2005]), the term "serrated distal ridge" seems appropriate.

Potential synapomorphies (related with the mouthparts) for at least *Synaphris* could be the **scarce number of maxillary setae** around the labrum and labium and the **clavate setae** on the distal maxillae (fig. 5). These features seem to be rare among spiders (Martín J. Ramírez, personal commun.)

The **dorsal translucent expansion of the embolar base** (the embolic lamella) is a putative synapomorphy for at least *Synaphris*, as no embolic lamella seems to be present in the palp of *Cepheia longiseta* (Thaler and Noflatscher, 1990 figs. 25–27; Lopardo and Hormiga, in press; contra Marusik and Lehtinen, 2003). This embolic lamella is also absent in males of mysmenid and anapid spiders (LL, unpubl. data). It seems that other *Synaphris* species, besides *S. orientalis, S. lehtineni*, and *S. saphrynis*, n.sp., might have an embolic lamella (e.g., *S. letourneuxi* and *S. dalmatensis*: i.e., the *letourneuxi* group, Marusik and Lehtinen, 2003; also the two new Malagasy *Synaphris* species, Miller, in press). SEM studies are needed for the *calerensis* group (*S. calerensis, S. agaetensis* and *S. franzi*). The homology of the embolic lamella with the theridiid conductor (at least in *Theridion*, arising from the embolar base, Marusik and Lehtineni, 2003) remains untested. Also, the term "lamella" is widely used for structures that are unlikely to be homologous to the membrane found in Synaphridae (e.g., in Linyphiidae the lamella is a sclerite attached to the radix: the "lamella characteristica"; see Hormiga, 1994). We prefer to call the embolic "lamella" a "dorsal translucent expansion of the embolar base" until a proper homology statement is proposed.

The shape of the male palpal tibia, which is rounded retrolaterally and **pressed against the cymbial base**, appears to be synapomorphic for the family. However, the presence of **two pits** on the palpal tibia (Marusik and Lehtinen, 2003: 147, fig. 17) has not been properly described, but they appear to be two small depressions in the distal surface of the tibia that contain the cymbium. We cannot find such depressions in *S. saphrynis*, n.sp. Conversely, these cavities on the tibia seem to be absent in *Cepheia longiseta* (LL, personal obs.). For the discussion of the **embolar and cymbial conductors**, see *Palpal Morphology of* Synaphris.

The **notched tibial trichobothrial base** does not seem to be a synapomorphy for the family (as proposed by Marusik and Lehtinen, 2003, based on the study of *S. orientalis*; see also Miller, in press). A notched trichobothrial base is absent from the tibiae and the

←

Figs. 72–80. C*epheia longiseta*. Female paralectotype, spinnerets. **72.** Spinning field, ventral view; **73.** Same, posterior view; **74.** Right anterior lateral spinneret; **75.** Left anterior lateral spinneret; **76.** Right posterior median spinneret; **77–78.** Left posterior median spinneret; **79–80.** Left posterior lateral spinneret. Abbreviations are spelled out in appendix 1.

metatarsi of *S. saphrynis*, n.sp. Instead, we observed a smooth crescent-shaped, hooded trichobothrial base in both tibiae and metatarsi, as it is known from some other Araneoidea (see Miller, in press). The basal hood presents one lateral ridge on each side, which seems synapomorphic for the family as well. The same smooth trichobothrial base seems to be present in *S. lehtineni* and the Malagasy *Synaphris* species, further suggesting the autapomorphic nature of such condition in *S. orientalis*.

Another family-level diagnostic character is the **pseudosegmentation of the tarsi** (Marusik et al., 2005). None of the tarsi that we have studied using SEM for *S. saphrynis*, n.sp. is pseudosegmented. Miller (in press) found tarsus pseudosegmentation in the three studied synaphrid species. This character may define clades within the family.

Tarsi and metatarsi relative lengths seem to vary across symphytognathoids. According to Marusik and Lehtinen (2003) "the tarsi of all Synaphridae are longer than the metatarsi." A closer examination of the relative length of these leg articles across synaphrid taxa reveals that it is not always the case. Furthermore, the statistical significance of "longer" versus "shorter" is neither calculated nor discussed. In their description of *S. orientalis*, only measurements of the lengths of segments on leg I are provided, and in this species tarsus I does seem to be longer (ta 0.29/mt 0.24), although no other measurements of additional legs are given. For tarsus/metatarsus I, tarsi also seem to be longer in *S. calerensis* (0.22/0.19), *S. franzi* (0.23/0.18), and the females of *S. dalmatensis* (0.30/0.27; Wunderlich, 1980, 1987). Metatarsi seem to be longer than tarsi in *S. agaetensis* (leg I: ta 0.18/mt 0.23), the male of *S. dalmatensis* (leg I: 0.21/0.24; Wunderlich, 1980, 1987), and *S. letourneuxi* (leg I: 0.29/0.32; II: 0.29/0.32; III: 0.24/0.29; IV: 0.27/0.29; Brignoli, 1970). In the case of *S. lehtineni*, according to table 1 in Marusik et al. (2005), the tarsi seem to be slightly longer than metatarsi only for leg I, whereas tarsi of the other legs seem equal in length to the corresponding metatarsi. In *S. saphrynis*, n.sp. the tarsi seem to be slightly longer than metatarsi on legs I and II, but equally long on legs III and IV (table 1). In the case of *Cepheia longiseta*, in both sexes the tarsi and metatarsi are of equal length, except for the leg III, where the metatarsus is shorter (0.20/0.16) (Brignoli, 1970). In conclusion, as no statistical tests were carried out in any of these cases, we suspect that if such differences in length were tested, they would turn out to be not significant. As Simon (1894: 589) stated in his original description of *Synaphris*, the tarsi and metatarsi are almost equally long.

Regarding the spinneret spigot morphology, the reduction of the furrow separating the ampullate and piriform fields seem to be synapomorphic for Synaphridae. Also, while not unique to Synaphridae, the potential retention of triplet spigots in adult synaphrid males might be characteristic for the family (see Miller, in press). Finally, if the retention of two of the three triad spigots hold, the loss of one aggregate spigot in the PLS triplet might be synapomorphic for the family as well, as proposed by Miller (in press).

In conclusion, putative synapomorphies for *Synaphris* and/or Synaphridae include: a distinct constriction on the tarsus-metatarsus joints; a cheliceral keel ending in a strong promarginal cheliceral tooth; scarce number of maxillary setae; distal maxillary setae clavate; and a characteristic palpal morphology, comprising a distinctive tibial morphology (rounded retrolaterally and pressed against the cymbial base), a modified cymbium with two distinct areas (a sclerotized one bearing setae, and a glabrous membranous one), a palpal dorsal translucent expansion of the embolar base (embolic "lamella"), a retrolateral paracymbium, and a reduced furrow separating the MAP from the piriform field. Refuted synapomorphies for the genus or the family are the metatarsal subdistal anastomosed lyriform organ, the notched tibial trichobothrial base, and the tarsal pseudosegmentation.

The Position of Synaphridae

Marusik and Lehtinen (2003) provided a detailed discussion about the potential placement of Synaphridae within Araneoidea. They concluded that synaphrids were not nested within mysmenids and discussed the exclusion of the Synaphridae from the Symphytognathoidea (contra Wunderlich, 1986, 1995 and Schütt, 2003). They also concluded that the family is not related to micropholcommatids, and although the shape of the lateral surface of the palpal tibia (developed into a rounded lobe) is present in most theridiids, "…this group [Synaphridae] cannot be placed in any family to which it has been assigned during its history (Theridiidae, Mysmenidae, Symphytognathidae, and Anapidae), because it lacks the generally accepted synapomorphies of all these groups" (Marusik and Lehtinen, 2003: 147). They also mentioned a similarity with the Cyatholipidae based on the position of the tarsal organ (ca. 0.36), but they did not propose a formal hypothesis of relationship.

Surprisingly Marusik and Lehtinen (2003: 151) proposed that the genus *Synaphris* is related to *Theridion* (Theridiidae): "It seems that *Synaphris* is related to or at least more similar to Theridiidae (Theridiinae, *Theridion*). Common (similar) characters are as follows: 1) a circular base of the embolus, 2) tip of the embolus terminal in relation to the tegulum, 3) internal 'paracymbium', 4) circular margin of the palpal tibia covering basal part of the cymbium and the bulb, 5) the conductor (= embolic lamella in *Synaphris*) originating from under the embolus base". We consider that the sharing of these features might not be unique to *Synaphris*-*Theridion*, and therefore do not allow for the suggestion of a close relationship. Furthermore, such a proposal would require one to empirically demonstrate that *Synaphris* shares the synapomorphies of Theridiidae (see Discussion above). The typical theridiid tarsal comb on leg IV is absent in *Synaphris saphrynis*.

The position of Synaphridae within Araneomorphae is controversial due to sets of characters that support contradicting placements. On the one hand, the presence of a paracymbium in *Synaphris* suggests a potential placement within Araneoidea, although not close to Theridiidae, which lacks a basal paracymbium. The anterior respiratory system transformed into tracheae, although present in Caponiidae, within Araneoidea seems exclusive to symphytognathoids (Schütt, 2003; Griswold et al., 1998) and further supports (or at least does not refute) a placement of the family within Araneoidea. The same conclusion can be reached from the anastomosed lyriform organs in the distal metatarsi, which appear to be present in symphytognathoids as well as in theridiids and uloborids, and might be common within orbicularians. On the other hand, the weak furrow between the major ampullate and the piriform spinning fields (considered absent by Schütt, 2003) contradicts the placement of Synaphridae within Araneoidea (or suggest instances of homoplasy) and therefore the spinneret morphology might place Synaphridae in a different position (as a non-araneoid) than previously thought.

The broad posterior tracheal spiracle (i.e., two distant spiracles connected by a furrow), the retention of PLS triplet spigots in the adults males, and the absence of female palpal claw (at least in *Cepheia* females, LL personal obs.; also in the Malagasy species, Miller, in press) are some of the proposed synapomorphies of the araneoid family Cyatholipidae (Griswold, 2001). The truncated posterior sternum margin and the absence of median apophysis on male palps, while common among symphytognathoids, are also characteristic not only for the cyatholipids but also for its sister group, the family Synotaxidae (Griswold, 2001). Furthermore, a posterior respiratory system similar to that of *Synaphris* (two main tracheal bundles from two connected atria, with the tracheoles directed mainly anteriorly and reaching into the prosoma, i.e., desmitracheate) has been previously described for Cyatholipidae (Davies, 1978; Forster, 1980, 1988; Griswold, 2001) and for some groups of Linyphiidae (Blest, 1979; Millidge, 1986, 1988; Hormiga, 1994, 2000). The cyatholipid and linyphiid (mainly, but not exclusively, in the subfamily Erigoninae) tracheal systems include lateral tracheae arising from a less deep atrium (e.g., Forster, 1988: figs. 19–20; Hormiga, 2000: fig. 31G), which seems to be different from that in *Synaphris*. The apodemal lobes present in cyatholipids (Forster, 1988 figs. 19–20; Griswold, 2001 figs. 12A–C) are also absent in *Synaphris*. The presence of several of the proposed cyatholipid synapomorphies in synaphrids may suggest a close relationship to this araneoid family. Of course, this conjecture needs to be tested within the context of a cladistic analysis with the appropriate taxonomic sample. The study of new synaphrid species as well as potential outgroup taxa will test the hypotheses of homology that we have described as well as the cladistic position of the family.

ACKNOWLEDGMENTS

Many thanks to the members of the project "Evaluating current European agri-environment schemes to quantify and improve nature conservation efforts in agricultural landscapes (EASY)" (Kleijn et al., 2006), especially to José Luis Yela García (Spain), for providing the specimens of *Synaphris*. We also would like to thank Christine Rollard and Elise-Anne Leguin (MNHN) for the loan of *Cepheia longiseta* and for granting permission for its SEM study. Thanks to John Murphy (U.K.) for his distribution data of *Cepheia longiseta*. Thanks to Norman Platnick, Jeremy Miller, and Yuri Marusik for comments on early drafts of this article. Special thanks to Jeremy Miller for enlightening discussions, and for kindly sharing his unpublished data and previous versions of his manuscript, and to Martín J. Ramírez for priceless discussions on spinneret spigot morphology. We thank Charles Griswold and Bernhard Huber for useful comments and critical reading of the manuscript. Funding for this research has been provided by grants from the U.S. National Science Foundation (DEB-0328644 to G. Hormiga and G. Giribet and EAR-0228699 to W. Wheeler, J. Coddington, G. Hormiga, L. Prendini and P. Sierwald) and by a George Washington University REF grant to G.H.

REFERENCES

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological Journal of the Linnean Society 141: 447–626.

Benjamin, S.P., and S. Zschokke. 2004. Homology, behaviour and spider webs: web construction behaviour of *Linyphia hortensis* and *L. triangularis* (Araneae: Linyphiidae) and its evolutionary significance. Journal of Evolutionary Biology 17: 120–130.

Bertkau, P. 1890. Arachniden gesammelt vom 12. November 1888 bis zum 10. Mai 1889 in San Remo von Prof. Dr Oskar Schneider, 1–11.

Blest, A.D. 1979. The spiders of New Zealand. Part V. Linyphiidae-Mynogleninae. Otago Museum Bulletin 5: 95–173.

Brignoli, P.M. 1970. Contribution à la connaissance des Symphytognathidae paléarctiques (Arachnida, Araneae). Bulletin du Muséum National d'Histoire Naturelle 41: 1403–1420.

Davies, V.T. 1978. A new family of spiders (Araneae: Teemenaaridae). Symposia of the Zoological Society of London. 42: 293–302.

Denis, J. 1933a. Chasses arachnologiques dans les Pyrenees-Orientales (Region de Banyuls-sur-Mer et Vallespir). Bulletin de la Société d'histoire naturelle de Toulouse 65: 529–591.

Denis, J. 1933b. Quelques araignées nouvelles pour le département du Var. Bulletin de la Société Entomologique de France 38: 329–331.

Dingerkus, G., and L.D. Uhler. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. Stain Technology 52(4): 229–232.

Forster, R.R. 1980. Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. Proceedings of the VIII International Congress of Arachnology (Verh. int. arachnol. Kong. 8, Wien, 1980): 269–284.

Forster, R.R. 1988. The spiders of New Zealand: Part VI. Family Cyatholipidae. Otago Museum Bulletin 6: 7–34.

Griswold, C.E. 2001. A monograph of the living world genera and Afrotropical species of cyatholipid spiders (Araneae, Orbiculariae, Araneoidea, Cyatholipidae). Memoirs of the California Academy of Sciences 26: 1–251.

Griswold, C.E., J.A. Coddington, G. Hormiga, and N. Scharff. 1998. Phylogeny of the orb web building spiders (Araneomorphae, Orbiculariae). Zoological Journal of the Linnean Society 123: 1–99.

Griswold, C.E., M.J. Ramírez, J.A. Coddington, and N.I. Platnick. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae, Araneomorphae, Entelegynae), with comments on their phylogeny. Proceedings of the California Academy of Sciences, 4th ser. 56, suppl. II: 1–324.

Hormiga, G. 1994. Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). Zoological Journal of the Linnean Society 111: 1–71.

Hormiga, G. 2000. Higher level phylogenetics of erigonine spiders (Araneae, Linyphiidae, Erigoninae). Smithsonian Contributions to Zoology 609: 1–160.

Hormiga, G. 2003. *Weintrauboa,* a new genus of pimoid spiders from Japan and adjacent islands, with comments on the monophyly and diagnosis of the family Pimoidae and the genus *Pimoa* (Araneoidea, Araneae). Zoological Journal of the Linnean Society 139: 261–281.

Hormiga, G., D.J. Buckle, and N. Scharff. 2005. *Nanoa*, an enigmatic new genus of pimoid spiders from western North America (Pimoidae, Araneae). Zoological Journal of the Linnean Society 145: 249–262.

Hormiga, G., and N. Scharff. 2005. Monophyly and phylogenetic placement of the spider genus *Labulla* Simon, 1884 (Araneae, Linyphiidae) and description of the new genus *Pecado*. Zoological Journal of the Linnean Society 143: 359–404.

Kaston, B.J. 1978. How to know the spiders, 3rd ed. Dubuque, Iowa: Wm. C. Brown, 272 pp.

Kleijn, D., R.A. Baquero, Y. Clough, M. Diaz, J. de Esteban, F. Fernández, F. Herzog, A. Holzschuh, E. Knop, A. Kruess, E.J.P. Marshall, I. Steffan-Dewenter, T. Tscharntke, J. Verhulst, T.M. West, and J.L. Yela. 2006. Mixed biodiversity benefits of agri-environment schemes implemented in contrasting European countries. Ecology Letters 9: 243–254.

Lopardo, L. 2005. Phylogenetic revision of the spider genus *Negayan* (Araneae, Anyphaenidae, Amaurobioidinae). Zoologica Scripta 34: 245–277.

Lopardo, L., and G. Hormiga. In press. On the synaphrid spider *Cepheia longiseta* (Simon 1881) (Araneae, Synaphridae). American Museum Novitates.

Marusik, Y.M., and P.T. Lehtinen. 2003. Synaphridae Wunderlich, 1986 (Aranei: Araneoidea), a new family status, with a description of a new species from Turkmenistan. Arthropoda Selecta 11: 143–152.

Marusik, Y.M., V.A. Gnelitsa, and M.K. Kovblyuk. 2005. A new species of *Synaphris* (Araneae, Synaphridae) from Ukraine. Bulletin of the British Arachnological Society 13: 125–130.

Medan, V. 2001. On the genus *Eilica* (Araneae, Gnaphosidae) from Argentina. Journal of Arachnology 29: 423–426.

Miller, J.A. In press. Synaphridae of Madagascar (Araneae: Araneoidea): a new family record for the Afrotropical Region. Proceedings of the California Academy of Sciences.

Millidge, A.F. 1986. A revision of the tracheal structures of the Linyphiidae (Araneae). Bulletin of the British Arachnological Society 7: 57–61.

Millidge, A.F. 1988. The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae). Bulletin of the British Arachnological Society 7: 253–268.

Platnick, N.I. 1975. A revision of the spider genus *Eilica* (Araneae, Gnaphosidae). American Museum Novitates 2578: 1–19.

Platnick, N.I. 2006. The world spider catalog, version 7.0. American Museum of Natural History, online at http://research.amnh.org/entomology/spiders/catalog/index.html

Platnick, N.I., J.A. Coddington, R.R. Forster, and C.E. Griswold. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1–73.

Platnick, N.I., and R.R. Forster. A revision of the temperate South American and Australasian spiders of the family Anapidae (Araneae, Araneoidea). Bulletin of the American Museum of Natural History, 190: 1–139.

Schütt, K. 1995. *Drapetisca socialis* (Araneae: Linyphiidae): web reduction - ethological and morphological adaptations. European Journal of Entomology 92(3): 553–563.

Schütt, K. 2003. Phylogeny of Symphytognathidae s.l. (Araneae, Araneoidea). Zoologica Scripta 32: 129–151.

Simon, E. 1881. Les arachnides de France. Paris, 5: 1–180.

Simon, E. 1894. Histoire naturelle des araignées. Paris, 1: 489–760.

Simon, E. 1926. Les arachnides de France. Synopsis générale et catalogue des espèces françaises de l'ordre des Araneae; 2e partie. Paris, 6: 309–532.

Szüts, T., and R. Jocqué. 2001. A revision of the afrotropical spider genus *Palfuria* (Araneae, Zodariidae). Journal of Arachnology 29: 205–219.

Thaler, K. 1993. Beiträge zur Spinnenfauna von Nordtirol—2. Veröffentlichungen des Museum Ferdinandeum 73: 69–119.

Thaler, K., and M.-T. Noflatscher. 1990. Neue und bemerkenswerte Spinnenfunde in Südtirol (Arachnida: Aranei). Veröffentlichungen des Museum Ferdinandeum Innsbr. 69: 169–190.

Ubick, D., P. Paquin, and P.E. Cushing. 2005. Glossary and pronunciation guide. *In* D. Ubick, P. Paquin, P.E. Cushing and V. Roth (editors), Spiders of North America: an identification manual: 260–273. American Arachnological Society.

Wunderlich, J. 1980. Über europäische Symphytognathidae (Arachnida: Araneae). Verhandlungen des naturwissenschaftlichen Vereins in Hamburg (Neue Folge) 23: 259–273.

Wunderlich, J. 1986. Die Beziehungen fossiler und rezenter Radnetzspinnen-Verwandter (Überfamilie Araneoidea). *In* Spinnenfauna gestern und heute: Fossile Spinnen in Bernstein und ihre heute lebenden Verwandten, 93–135. Wiesbaden: Quelle and Meyer, 283 pp.

Wunderlich, J. 1987. Die Spinnen der Kanarischen Inseln und Madeiras: Adaptive Radiation, Biogeographie, Revisionen und Neubeschreibungen. Taxonomy &. Ecology 1: 1–435.

Wunderlich, J. 1995. Die Beziehungen der Synaphrinae Wunderlich 1986 (Araneae: Anapidae); Beiträge zur Araneologie, 4: 775–776.

APPENDIX 1

ANATOMICAL ABBREVIATIONS

AC	aciniform gland
AG	aggregate gland
ALE	anterior lateral eye(s)
ALS	anterior lateral spinneret
AME	anterior median eye(s)
C	conductor
Cap	apophysis of conductor
CB	cymbium
cs	chemosensory seta
CY	cylindrical gland
E	embolus
EB	embolar base
EP	embolar process (embolic lamella)
FL	flagelliform gland
LE	lateral eyes
MAP	major ampullate gland
mt	metatarsus
n	nubbin
P	paracymbium
PI	piriform gland
PLE	posterior lateral eye(s)
PLS	posterior lateral spinneret(s)
PME	posterior median eye(s)
PMS	Posterior median spinneret(s)
t	tartipore
ta	tarsus

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site http://library.amnh.org/pubs. Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.