

**SYSTEMATICS OF THE AFRO-MACARONESIAN  
SPIDER GENUS *SANCUS*  
(ARANEAE, TETRAGNATHIDAE)**

**Matjaž Kuntner**<sup>1,2</sup> and **Fernando Alvarez-Padilla**: Department of Biological Sciences, George Washington University, 2023 G St. N.W., Washington, D.C. 20052, USA; and Department of Entomology, National Museum of Natural History, Smithsonian Institution, NHB-105, PO Box 37012, Washington, D.C. 20013–7012, USA

**ABSTRACT.** We review the systematics of the tetragnathid spider genus *Sancus* Tullgren, hitherto known from a single species from Kilimanjaro. The type species *Sancus bilineatus* Tullgren is redescribed and diagnosed from the only other known species, *S. acorensis* (Wunderlich) new combination. *Leucognatha* Wunderlich is a junior synonym of *Sancus*, which thus eliminates two monotypic tetragnathid genera. A phylogenetic analysis of 15 tetragnathid and eight outgroup genera confirms the monophyly of *Sancus* and places it precisely in Tetragnathidae. We discuss the phylogenetic relationships among tetragnathid genera and the peculiar biogeography of *Sancus*, now known from east African mountains (Kilimanjaro and Mt. Kenya) and from the Azores in the northeastern Atlantic.

**Keywords:** Tetragnathidae, *Sancus*, *Leucognatha*, taxonomy, phylogenetics, biogeography

No taxonomic treatment of the tetragnathid genus *Sancus* exists in the literature since Tullgren's (1910) original description of a species from Kilimanjaro and the genus has remained monotypic until now (Platnick 2004). The original description of *Sancus bilineatus* Tullgren 1910 included illustrations of both the epigynum and palpus (Tullgren 1910: figs. 87–88). However, the illustrations are insufficient to reliably confirm the placement of *Sancus* in Tetragnathidae. *Sancus* has traditionally been placed among the “metines” (“metids,” “Metinae”), a taxonomic concept often changing status and rank (see Taxonomic History). “Metines” have been shown to be a paraphyletic assemblage of tetragnathid genera nested between Nephilinae and Tetragnathinae (Hormiga et al. 1995). However, the

placement of *Sancus* has never been tested phylogenetically. We are currently studying the higher level phylogenetics of Tetragnathidae, with emphasis on taxa formerly classified as “metines” (Alvarez-Padilla & Hormiga in prep.) and on nephilines (Kuntner 2005, 2006a & b). Although the ‘metines’ are being recovered as monophyletic in our preliminary phylogenies, this name cannot be used, as the crustacean family name Metidae Boeck 1872 (based on *Metis* Philippi 1843), has priority over the spider family group name Metinae Simon 1894 (based on *Meta* C.L. Koch 1836).

Here, we reassess the validity and monophyly of the genus *Sancus*, provide a new diagnosis and circumscription, test its phylogenetic placement within the Tetragnathidae, redescribe the types of *S. bilineatus*, and propose *Leucognatha* Wunderlich 1992 (described as endemic in the Azores) as a junior synonym of *Sancus*. The genus is now known from east African mountains (Kilimanjaro and Mt. Kenya) and from the archipelago of the Azores in the northeastern Atlantic.

**Taxonomic history.**—Tullgren (1910) established the genus *Sancus* to accommodate a new species from Kilimanjaro, *S. bilineatus*

<sup>1</sup> Current address: Institute of Biology, Scientific Research Centre of the Slovenian Academy of Sciences and Arts, Novi trg 2, P.O. Box 306, SI-1001 Ljubljana, Slovenia. E-mail: huntner@gmail.com

<sup>2</sup> Since the acceptance of this paper, Kuntner (2005, 2006a & b) has presented newer analyses, which dispute the tetragnathid placement of nephilines, and elevate the clade (*Clitaetra*(*Herennia*(*Nephila* + *Nephilengys*)) to family rank, Nephilidae. However these new hypotheses do not affect *Sancus*.

Tullgren 1910. Following Simon's (1894) classification Tullgren listed *Sancus* within the family Argiopidae, which then included genera from the modern superfamily Araneoidea (see Griswold et al. 1998 for the current systematics). Further, Tullgren (1910) placed *Sancus* in Simon's group Meteae, close to the genera *Chrysometa* Simon and *Meta* Koch. Tullgren diagnosed *Sancus* from the other genera within the group by the straight posterior eye row. Petrunkevitch (1928) listed *Sancus* within the argioid subfamily Metinae. While Bonnet (1958) retained *Sancus* within Argiopidae, Roewer (1942) listed Metinae (including *Sancus*) within the Araneidae. Brignoli (1983) treated the Metidae (with *Sancus*) as a family, but Dippenaar-Schoeman & Jocqué (1997) list *Sancus* in Metinae (Tetragnathidae). *Sancus*, along with most genera from the group Meteae (*sensu* Simon) are now in the family Tetragnathidae (Platnick 2004).

*Leucognatha* Wunderlich 1992 was described as a monotypic genus (containing *L. acoreensis* Wunderlich 1992) endemic to the Azores archipelago in the northeastern Atlantic. *Leucognatha* was diagnosed, among other features, to lack femoral trichobothria, cheliceral denticles (between ridges), and median and terminal apophyses, and to possess a basal-retrodorsal outgrowth on male palpal cymbium (= cymbial basal process, see below) and a shallow groove frontally (= epigynal ventral depression, see below) on the distinctly sclerotized epigynum. Wunderlich (1992) placed *Leucognatha* in the tetragnathid subfamily Leucauginae (see Discussion). His description and illustrations of *L. acoreensis* prompted us to examine the type series for possible congeneric status with *Sancus*.

#### METHODS

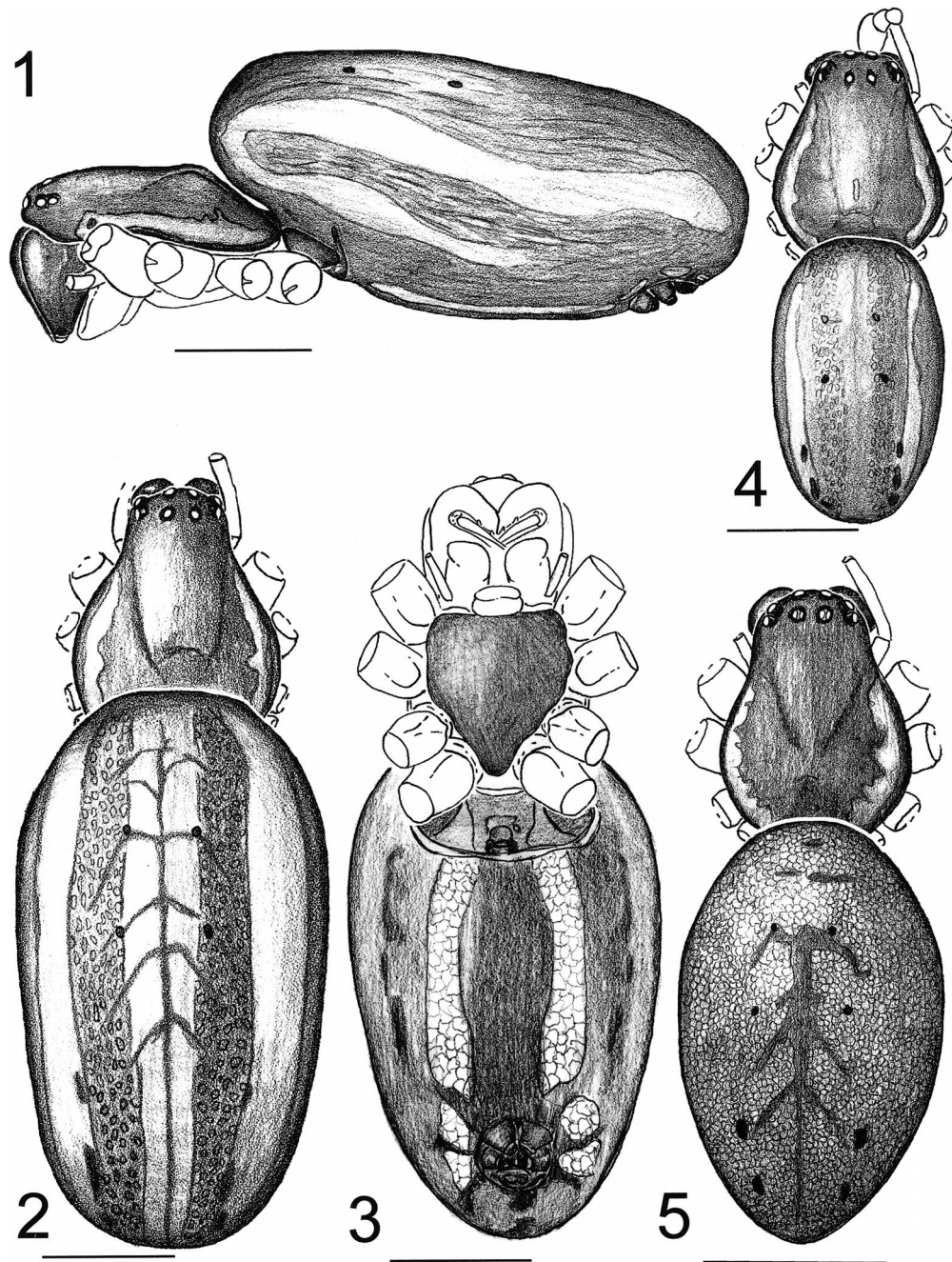
**Specimens.**—The types were borrowed from the collections of the Swedish Museum of Natural History (SMNH) in Stockholm and donated from Jörg Wunderlich's private collection (Straubenhardt, Germany). The latter were deposited in the collections of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. We examined the available identified and unidentified tetragnathids in the collections of USNM, the American Museum of Natural History (AMNH) in New York, and the Cal-

ifornia Academy of Sciences (CAS) in San Francisco. We found a single female *S. bilineatus* in USNM. In all other collections we failed to find *Sancus*. Additionally, *Sancus* is apparently absent from the following European museums with rich African collections: Royal Museum for Central Africa (RMCA), Tervuren, Belgium (R. Jocqué in litt.), Muséum national d'histoire naturelle (MNHN), Paris (own data), Museum fuer Naturkunde der Humboldt-Universitaet, Berlin (ZMB, J. Dunlop in litt.) and the British Museum of Natural History (BMNH), London (J. Beccaloni in litt.).

**Taxonomic methods.**—General taxonomic methods follow Hormiga (2002). Morphological observations and illustrations of external structures were made using a Leica MZ APO dissecting microscope with a camera lucida. Internal genitalic structures were cleared in methyl salicylate (Holm 1979), mounted on a temporary slide (Coddington 1983) and examined and illustrated under compound microscope Leica DMRM with a camera lucida. Measurements were taken using a reticle calibrated in millimeters. Illustrations were rendered on coquille board and scanned for digital manipulation in Adobe Photoshop 7.0. The maps were redrawn in Adobe Illustrator 10 from the Microsoft Encarta Interactive World Atlas 2000 templates. All plates were assembled and labeled in Adobe Illustrator 10.

**Anatomical abbreviations.**—ALE = anterior lateral eyes; AME = anterior median eyes; C = conductor; CB = cymbium; CBP = cymbial basal process; CO = copulatory opening; CP = epigynal caudal plate; E = embolus; FD = fertilization duct; P = paracymbium; PLE = posterior lateral eyes; PME = posterior median eyes; S = spermatheca; St = subtegulum; T = tegulum; TB = epigynal posterior transverse bar; VD = epigynal ventral depression.

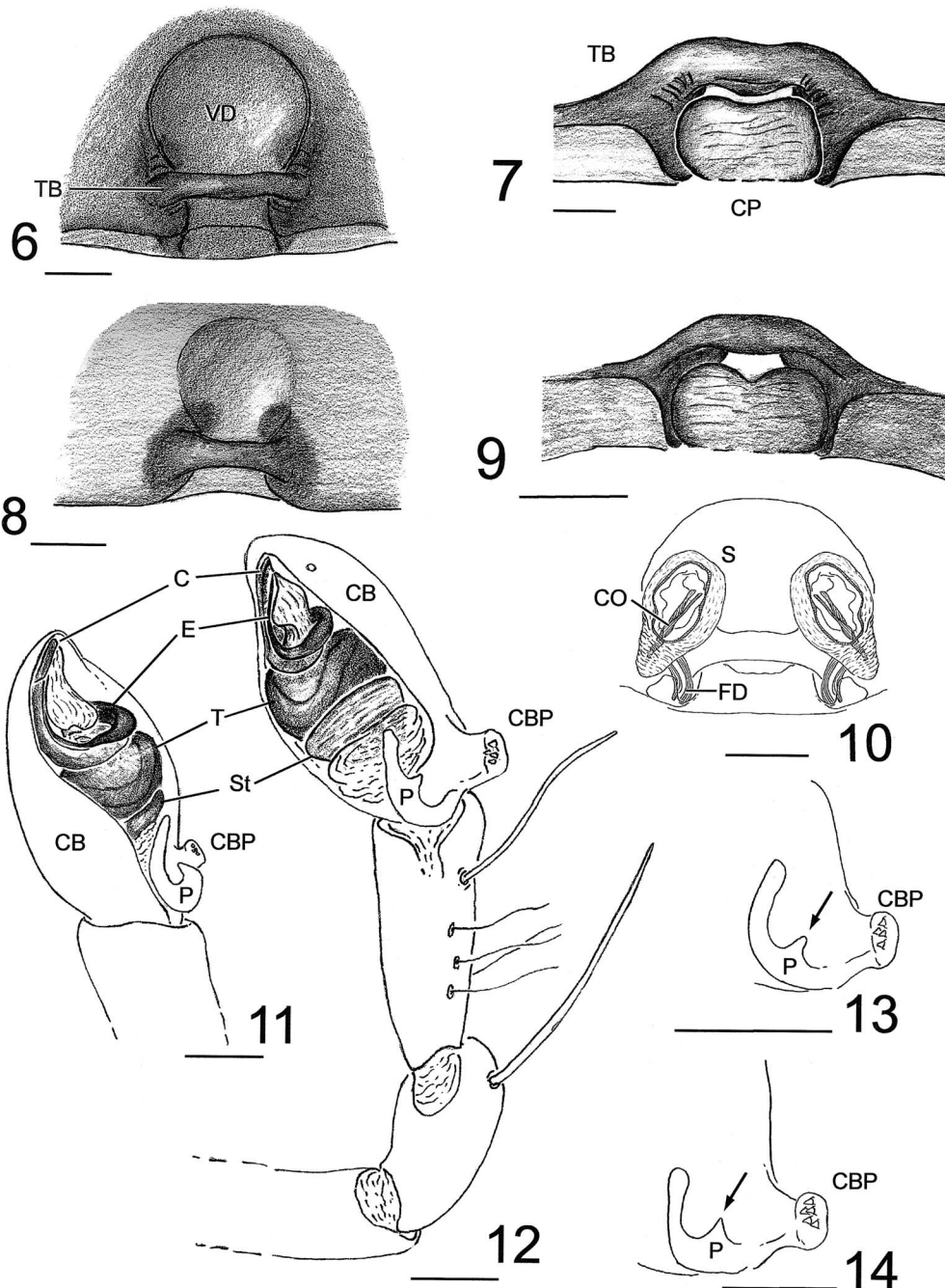
**Character analysis.**—The morphological examination of the two *Sancus* species implied the placement of the genus in the family Tetragnathidae. To test such phylogenetic placement and the monophyly of *Sancus*, we used the published data matrix of Hormiga et al. (1995) containing 14 tetragnathid genera plus eight genera from seven outgroup families (Table 1) scored for 60 morphological and behavioral characters. We coded both *Sancus* species for all 60 characters (Table 2) and add-



Figures 1–5.—*Sancus* somatic morphology. 1–4. *Sancus bilineatus*. 1–3. female syntype, lateral (1), dorsal (2), ventral (3); 4. male syntype, dorsal; 5. *Sancus acorensis*, female paratype, dorsal. Scale = 1.0 mm.

ed three new characters. These new characters, described below, are numbered as characters 61–63. The entries for *Sancus* behavior (characters 42–53) and the spinneret morphology (characters 54–60) remain missing

(marked as question marks) due to lack of data and specimens. Below, we explain selected character codings. While we point out some errors in Hormiga et al. (1995) we did not change the codings from that published



Figures 6–14.—*Sancus* genitalic morphology. 6, 7, 10. *S. bilineatus* female syntype epigynum, ventral (6), caudal (7), dorsal, cleared (10); 8, 9. *S. acoreensis*, female paratype epigynum, ventral (8), caudal (9); 11–13. *S. bilineatus* male syntype left palp, ventral (11), ectal (12), detail of paracymbium, paracymbial apophysis (arrow) and cymbial basal process, ectal (13); 14. *S. acoreensis*, male paratype, detail of paracymbium, paracymbial apophysis (arrow) and cymbial basal process, ectal. Scale = 0.1 mm. See Methods for anatomical abbreviations.

Table 1.—Terminal taxa from Hormiga et al. (1995) with the addition of *Sancus* species (this analysis).

Family	Taxon	Author and year
Uloboridae	<i>Uloborus</i>	Latreille 1806
Araneidae	<i>Araneus</i>	Clerck 1757
	<i>Argiope</i>	Audouin 1826
Linyphiidae	<i>Linyphia</i>	Latreille 1804
Pimoidae	<i>Pimoida</i>	Chamberlin & Ivie 1943
Theridiidae	<i>Steatoda</i>	Sundevall 1833
Nesticidae	<i>Nesticus</i>	Thorell 1869
Theridiosomatidae	<i>Epeirotypus</i>	O. P.-Cambridge 1894
Tetragnathidae	<i>Phonognatha</i>	Simon 1894
	<i>Clitaetra</i>	Simon 1889
	<i>Nephila</i>	Leach 1815
	<i>Herennia</i>	Thorell 1877
	<i>Nephilengys</i>	L. Koch 1872
	<i>Azilia</i>	Keyserling 1881
	<i>Dolichognatha</i>	O. P.-Cambridge 1869
	<i>Meta</i>	C. L. Koch 1836
	<i>Chrysometa</i>	Simon 1894
	<i>Metellina</i>	Chamberlin & Ivie 1941
	<i>Leucauge</i>	White 1841
	<i>Tetragnatha</i>	Latreille 1804
	<i>Glenognatha</i>	Simon 1887
	<i>Pachygnatha</i>	Sundevall 1823
	<i>Sancus bilineatus</i>	Tullgren 1910
<i>Sancus acorensis</i>	(Wunderlich 1992)	

matrix as such revision was beyond the scope of this paper and will be done elsewhere.

*Character 21:* (erroneously labeled as Ch. 22 in Hormiga et al. 1995: 329). Cymbium orientation in *Sancus* is mesal (Fig. 4). At least nephilines and certain ‘metines’ were miscoded in Hormiga et al. (1995) as they also exhibit the ‘araneid’ mesal orientation.

*Character 25:* *Sancus* has the paracymbial secondary process (Hormiga et al. 1995: fig. 6B) and it is procurved. We think the feature is better termed the cymbial basal process (CBP, Figs 11–14) because it arises from the cymbial base rather than from the paracymbium.

*Character 31:* The character state ‘‘a close association between the conductor and embolus, usually coiling together’’, a synapomorphy of Tetragnathidae (Hormiga et al. 1995), is difficult to interpret and needs redefinition. In most tetragnathines the embolus and the conductor indeed spiral (e.g. Levi 1980: figs. 174–176). In nephilines the conductor fully encloses the embolus (e.g. Levi 1980: figs. 25, 26; Hormiga et al. 1995: figs. 8A, 9A, 10A; Kuntner 2005, 2006a & b), exhibits little spiraling, and may not be homol-

ogous to the tegular conductor (Kuntner et al. in prep.). The condition in ‘‘metines’’ is diverse (Levi 1980; Hormiga et al. 1995: figs. 13A–H; Alvarez-Padilla in prep.). The conductor and the embolus of *Sancus* are closely associated: the conductor is grooved to hold the embolus in place and the coiling conductor closely follows the coiling of the embolus, so it seems to fit the first tetragnathid synapomorphy.

*Character 61:* Cymbial basal process apical denticles. 0: absent. 1: present (Figs 11–14). The feature is present in *Sancus*, absent in other tetragnathid genera with a CBP (*Dolichognatha*, *Meta*, *Chrysometa*, *Metellina*) and inapplicable for the remaining taxa. A cymbial denticulate process is typical of *Pimoida* (Pimoidae; Hormiga 1994: fig. 11). Although somewhat similar to the *Sancus* cymbial basal process, the cymbial process of *Pimoida* is positioned further apically on the cymbium and has no association with the paracymbium. We agree that *Pimoida* lacks the CBP (or paracymbium secondary process) and therefore this character is inapplicable in *Pimoida*.

*Character 62:* Epigynal transverse bar. 0: absent. 1: present (Figs. 6–9, TB). The feature

Table 2.—Coding of morphological and behavioral characters for both *Sancus* species.

<i>S. bilineatus</i>	001???11000?0000-0001101111100110000001000????????????????????111
<i>S. acoreensis</i>	0011111000?0000-0001101111100110000001000????????????????????111

occurs in *Sancus*, but is absent in all other terminals or inapplicable for haplogyne taxa.

**Character 63:** Epigynal ventral depression. 0: absent. 1: present (Figs. 6, 8, VD). The feature occurs in *Sancus*, but is absent in all other terminals or inapplicable for haplogyne taxa.

**Phylogenetic analysis.**—The matrix analyzed here had a total of 24 taxa (Table 1) scored for 63 characters. The parsimony analyses were performed using the computer programs NONA version 2.0 (Goloboff 1993) and PAUP\*4.0b.10 (Swofford 2002). In NONA we used search parameters ‘hold 1000’, ‘mult\*500’, ‘max\*’, and ‘sswap’, under ‘amb-’ and ‘amb =’. In PAUP we used random taxon addition for 500 replicates and TBR branch swapping. Winclada 1.00.08 (Nixon 2002) was used to display and manipulate trees and matrices for NONA. The multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch 1971). Successive character weighting (Farris 1969) was performed in PAUP based on the maximum value of the rescaled consistency index, base weight of 1. The bootstrap values were calculated in Winclada with 1000 iterations, each iteration with the search parameters ‘hold 500’, ‘mult\*50’, ‘max\*’. Bremer support or decay index values (Bremer 1988, 1994) were calculated in NONA using the command ‘bs10’ and ‘hold 100000’.

#### TAXONOMY

Family Tetragnathidae Menge 1866

Genus *Sancus* Tullgren 1910

*Sancus* Tullgren 1910: 152. Type species, by monotypy, *Sancus bilineatus* Tullgren.

*Sancus*: Petrunkevitch 1928: 142; Roewer 1942: 922; Bonnet 1958: 3928; Brignoli 1983: 226; Dippenaar-Schoeman & Jocqué 1997: 292, 338; Platnick 2004.

*Leucognatha* Wunderlich 1992: 359. Type species, by original designation, *Leucognatha acoreensis* Wunderlich NEW SYNONYMY.

**Diagnosis.**—*Sancus* can be diagnosed from all other tetragnathids by the combination of the following characters: denticulated male cymbial basal process (Figs. 11–14), sclero-

tized epigynum with a ventral depression and a transverse bar (Figs. 6–9), and absence of femoral trichobothria.

**Description.**—*Female*: General somatic morphology as in Figs. 1–3, 5. Cephalothorax with a narrow and low head region and elevated thoracic region (Figs. 1, 2, 5). Carapace glabrous. Carapace color (in alcohol) yellow to brown with two conspicuous lateral white lines (Figs. 2, 5). Sternum roughly heart-shaped, brown (Fig. 3). Labium as long as wide, rebordered (Fig. 3). Endites 2.5 times as long as wide. Anterior eye row slightly recurved, posterior eye row straight (Figs. 2, 5). Lateral eyes on a tubercle, almost juxtaposed, not widely separated from the medians (Figs. 1, 2, 5). Tapeta in secondary eyes present, canoe shaped (observed in *S. acoreensis* but not in *S. bilineatus* due to the specimen age). Chelicerae massive (Figs. 1, 3), with three prolateral and four (two large and two small) retrolateral teeth; cheliceral furrow not denticulated. Cheliceral boss (condyle) absent. Legs fairly short (see measurements below), with few spines. Femoral trichobothria absent. Leg formula 1-2-4-3. Abdomen cylindrical (Figs. 1–3, 5). Dorsum with silvery spots and with (*S. bilineatus*) or without (*S. acoreensis*) white lateral longitudinal lines. Venter with two longitudinal white lines and two paired white spots around the spinnerets (Fig. 3). Booklung covers smooth.

Epigynum (Figs. 6–9) is a well sclerotized ventral plate with an anterior depression (VD, Fig. 6, 8), a posterior transverse bar (TB, Figs. 6–9) and a caudal plate (CP, Figs. 7, 9). Internal epigynum morphology as in Fig. 10. Copulatory openings in the shape of slits laterally under the bases of the transverse bar (Fig. 10). The spermathecae wide apart, oval and well sclerotized (Fig. 10). Fertilization ducts arise from posterior part of spermathecae (Fig. 10).

*Male*: General somatic morphology illustrated in *S. bilineatus* (Fig. 4), resembles the female. Pedipalp (Figs. 11–14) with a single long patellar macroseta (Fig. 12). Palpal tibia long, with prolateral trichobothria (Fig. 12).

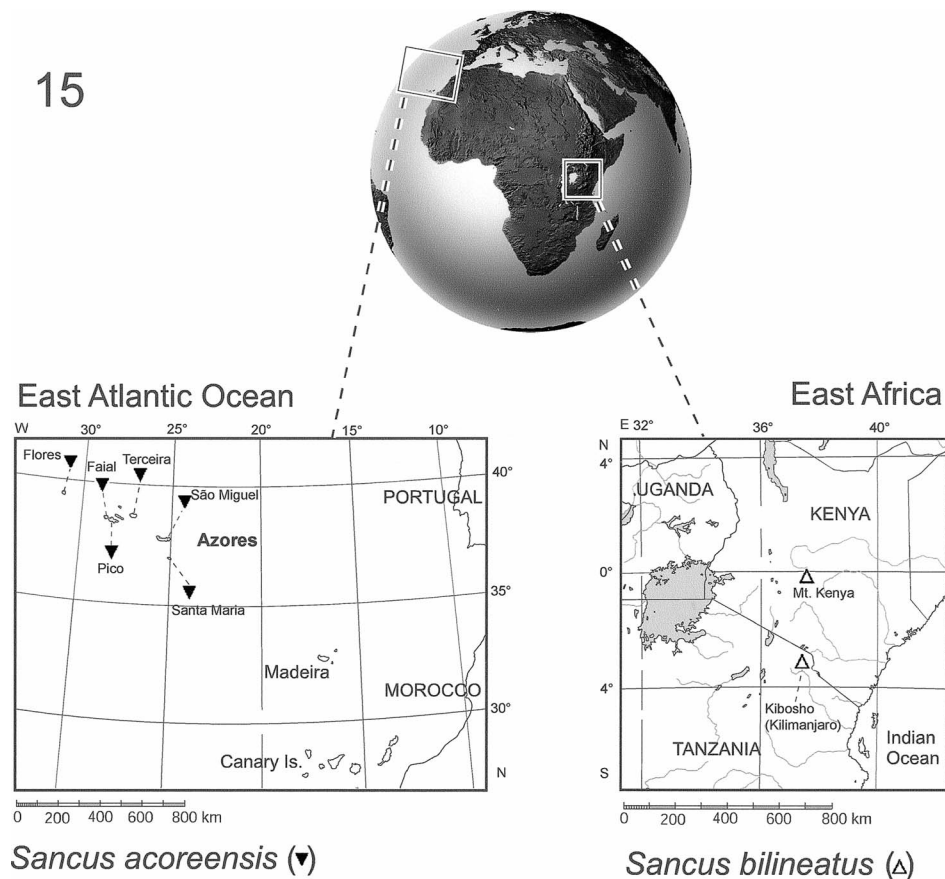


Figure 15.—World *Sancus* distribution. The genus is known from the Azores in the Atlantic Ocean (*S. acorensis*) and from the mountains of eastern Africa (*S. bilineatus*).

Cymbium long, tapering apically (Figs. 11, 12). Cymbial basal process present, with apical denticles (Figs 11–14). Paracymbium hook shaped (Figs 11–12), with a small mid-anterior process (Figs. 12–14), and no setae. Subtegulum as large as the globular tegulum (Fig. 12). Sperm duct without a switchback. Conductor (Figs. 11, 12), arising from the distal part of the tegulum, has a sclerotized and a membranous part, both holding the embolus in position. Embolus (Figs. 11, 12) sclerotized and wide, with no modifications.

**Composition.**—Two species: *Sancus bilineatus* Tullgren 1910 and *S. acorensis* (Wunderlich 1992) new combination.

**Comment on species diagnoses.**—The two *Sancus* species are best diagnosed by somatic features (size, abdomen shape and folium pattern) and less so by the genitalic morphology. While the ventral epigynal view is diagnostic

(Figs. 6, 8), the inner (dorsal) epigynum is uniform in both species. The difference between the palps of the species is subtle (detail of the paracymbial apophysis, see Figs. 13, 14).

**Distribution.**—East Africa, Azores (Fig. 15; also see Discussion).

**Natural History.**—Largely unknown (but see Ecology of each species).

*Sancus bilineatus* Tullgren 1910

Figs. 1–4, 6, 7, 10–13

*Sancus bilineatus* Tullgren 1910: 152, plate 3, figs. 87, 88 (♂♀ description (from Kilimanjaro). Syntypes in SMNH; examined; see comments below); Petrunkevitch 1928: 142; Roewer 1942: 922; Bonnet 1958: 3928; Brignoli 1983: 226; Platnick 2004.

**Material examined.**—We examined two males, three females and ten juveniles from

SMNH labeled "*Sancus bilineatus* Tullgr., Kilimandjaro, Kiboscho, Colleg. Lj. Sjst. Determ. A. T-n." Without a doubt these specimens are a part of the type series of *S. bilineatus*. Tullgren (1910:152) reported the type series collected during an expedition led by Y. Sjöstedt to the German East African territories as: "*Kilimandjaro*: Kiboscho, 3,000 Mtr., Febr. (18 ♂, ♀)" [= Kibosho, Tanzania, 3°14'S; 37°18'E]. The 15 syntypes available to us may represent only a part of the type series. Female chelicerae and two left male palps had been removed before our examination, yet the preserved material is in good condition.

**Other material examined.**—Kenya: 1 ♀, Mt. Kenya [approximate coordinates 0°08'S; 37°18'E], 16 Aug. 1970, D. Messersmith (USNM).

**Diagnosis.**—Females of *S. bilineatus* differ from those of *S. acoreensis* by the larger size (see variation), by the oval abdomen shape (Fig. 2), by the presence of longitudinal white lines on dorsum (Fig. 2), and by the epigynum with a large, well defined and well sclerotized anterior depression (Fig. 6). Males of *S. bilineatus* differ from those of *S. acoreensis* by the larger size (see variation), by the details of the paracymbium, which has a blunt apophysis (Fig. 13), and by the palpal tibial length, which is 2.5 times longer than wide (at its widest point).

**Description.**—*Female (syntype)*: Habitus as in Figs. 1–3. Total length 6.26. Cephalothorax 2.13 long, 1.75 wide, 0.75 high; yellow. Sternum 1.12 long, 0.94 wide; brown, darker at margins. Abdomen 4.56 long, 2.5 wide, 2.1 high; pale gray covered with white-silvery spots; dorsum with three longitudinal white lines (Fig. 2). Venter dark brown with two longitudinal white lines and four white spots around the spinnerets (Fig. 3). AME diameter 0.10. PME 0.12, ALE 0.08, PLE 0.08. AME separation 0.12, PME separation 0.13, AME-ALE separation 0.18. PME-PLE 0.16. Clypeus height 0.13. Legs yellow with white coxal spots. Leg I length 9.9, Leg II 8.4, Leg III 4.0, Leg IV 7.1, pedipalp length 2.3. Epigynum (Figs. 6, 7): Anterior depression deep and round, as wide as the transverse bar.

*Male (syntype)*: Habitus as in Fig. 4. Total length 3.6. Cephalothorax 1.68 long, 1.25 wide, 0.47 high; color as in female. Sternum 0.87 long, 0.7 wide; color as in female. Ab-

domen 2.18 long, 1.19 wide, 0.95 high; pale gray covered with white-silvery spots; dorsum with two longitudinal white lines (Fig. 4). AME diameter 0.10. PME 0.08, ALE 0.06, PLE 0.07. AME separation 0.08, PME separation 0.09. AME-ALE separation 0.14. PME-PLE separation 0.13. Clypeus height 0.1. Chelicerae teeth and leg pigmentation as in female. Leg I length 9.2, Leg II 7.0, Leg III 3.1, Leg IV 5.6, pedipalp 2.1. Pedipalp as in Figs. 11–13.

**Variation.**—Female total length ranges from 4.8 (Mt. Kenya) to 6.3 (Kilimanjaro), cephalothorax length from 1.4 (Mt. Kenya) to 2.4 (Kilimanjaro) ( $n = 4$ ). The epigynal caudal plate of the females from Kilimanjaro is narrow and only slightly notched (Fig. 7), while the caudal plate of the female from Mt. Kenya resembles that of *S. acoreensis* (Fig. 9). Male total length from 3.04–3.55, cephalothorax length from 1.68–1.90. The cymbial basal process can have four to six denticles and the number varies even within individuals.

**Distribution and ecology.**—Known from the high altitude (3000 m) type locality on the southern slope of Mount Kilimanjaro, Tanzania and the unspecified locality on Mt. Kenya (Fig. 15).

*Sancus acoreensis* (Wunderlich 1992)

NEW COMBINATION

Figs. 5, 8, 9, 14

*Leucognatha acoreensis* Wunderlich 1992: 360, figs. 315–326 (♂♀ description (from Azores); male and female paratypes deposited in USNM; examined); Platnick 2004.

**Material examined.**—A male and a female paratype of *Leucognatha acoreensis* Wunderlich, with no specific locality label (but see Distribution) was donated by J. Wunderlich, deposited in USNM. No additional material was available for examination.

**Diagnosis.**—Females of *S. acoreensis* differ from those of *bilineatus* by the smaller size (see variation), by the egg-shaped abdomen (Fig. 5), by the absence of longitudinal white lines on dorsum (Fig. 5), and by the epigynum with a small, poorly defined and weakly sclerotized anterior depression (Fig. 8). Males of *S. acoreensis* differ from those of *bilineatus* by the smaller size (see variation), the detail of the paracymbium, which has a pointed



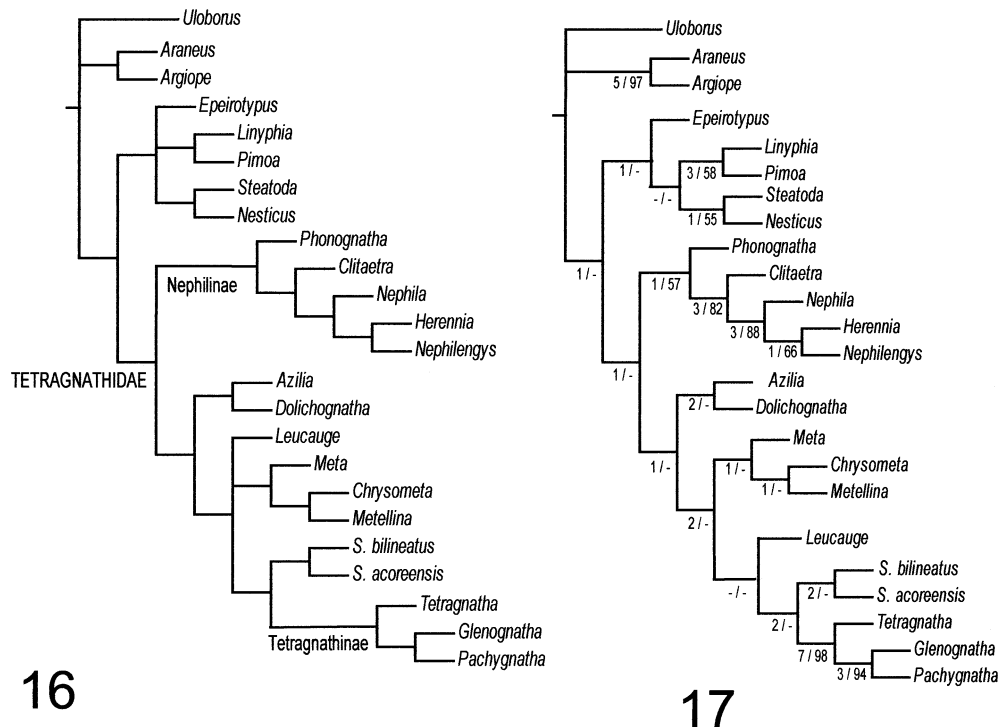


Figure 16.—Strict consensus of the six shortest cladograms (unweighted parsimony analysis). Family and subfamily names follow Hormiga et al. (1995). *Sancus bilineatus* and *S. acorensis* form a clade sister to tetragnathines.

Figure 17.—Preferred tetragnathid phylogeny with *Sancus* (a single successively weighted cladogram identical to one of the six fundamental cladograms). Branch support values given as Bremer/bootstrap, reported for values 1 and more for Bremer and for 50% and more for bootstrap.

apophysis (Fig. 14) and the tibial length, which is 1.7 times as long as wide.

**Description.**—*Female (paratype)*: Total length 3.9. Cephalothorax 1.56 long, 1.14 wide, 0.55 high; dark brown. Sternum 0.79 long, 0.78 wide; light brown, darker at margins. Abdomen 1.36 long, 1.66 wide, 1.7 high; dark gray covered with silver and golden spots (Fig. 5). AME diameter 0.10. PME 0.09, ALE 0.08, PLE 0.08. AME separation 0.10, PME separation 0.10. AME-ALE separation 0.08. PME-PLE separation 0.12. Clypeus height 0.10. Legs light brown. Leg I length 8.7, Leg II 7.0, Leg III 3.8, Leg IV 5.6, pedipalp length 1.9. Epigynum as in Figs. 8, 9: Anterior depression 0.8 times as wide as the transverse bar. Epigynal caudal plate wide and deeply notched (Fig. 9).

*Male (paratype)*: Total length 2.98. Cephalothorax 1.29 long, 0.90 wide, 0.44 high; color as in *S. bilineatus*. Sternum 0.7 long, 0.64

wide; color as in female. Abdomen 1.72 long, 1.0 wide, 1.04 high; dark gray covered with silvery spots and two longitudinal white-golden lines. AME diameter 0.09. PME 0.07, ALE 0.07, PLE 0.08. AME separation 0.09, PME separation 0.1. AME-ALE separation 0.12. PME-PLE separation 0.11. Clypeus height 0.09. Cheliceral teeth and leg pigmentation as in female. Leg I length 8.7, Leg II 6.7, Leg III 3.4, Leg IV 5.4, pedipalp length 1.6. Pedipalp as in *S. bilineatus* except for the diagnostic characters (see above).

**Variation (from Wunderlich 1992).**—Female total length ranges from 3.8–4.3, cephalothorax length from 1.45–1.55. Male total length from 2.5–3.2, cephalothorax length from 1.2–1.5.

**Distribution.**—Azores (Fig. 15): São Miguel, Santa Maria, Fajal, Pico, Terceira, Flores (Wunderlich 1992).

**Ecology.**—In Azores the spiders live in

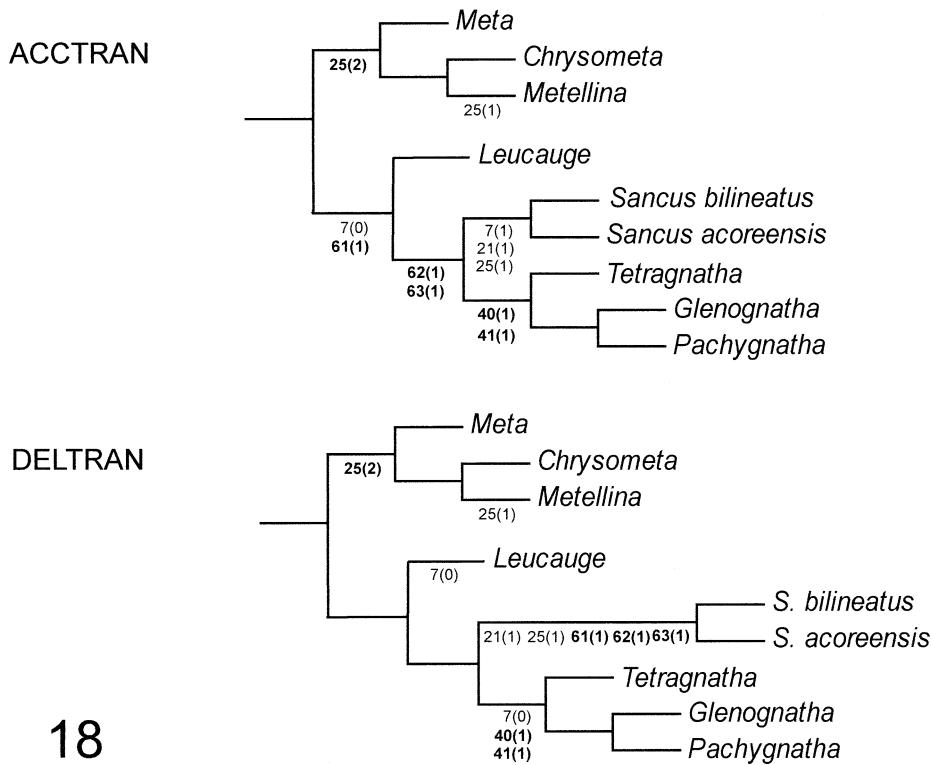


Figure 18.—Alternative optimizations of *Sancus* synapomorphies and other relevant characters and states (in parentheses) on the preferred phylogeny. Bolded are non-homoplasious characters. Delayed transformation (DELTRAN) is the preferred and more logical optimization (see text for details).

sunny to shaded upper vegetation layers near lakes (Wunderlich 1992:360). They were collected by beating vegetation and thus their webs are not known (Wunderlich in litt.).

#### PHYLOGENETICS

Heuristic searches in NONA produced two trees of minimal length under amb-, representing a subset of six minimal length trees in NONA under amb= and in PAUP. All minimal length topologies (length 136, CI = 0.56, RI = 0.72) have in common the placement of *Sancus* within Tetragnathidae, as well as the monophyly of *Sancus* and of Tetragnathidae. These results are congruent with those of Hormiga et al. (1995). Figure 16 shows the strict consensus of the six shortest trees. *Sancus* is recovered as sister to the tetragnathine clade (as defined by Hormiga et al. 1995) containing the genera *Tetragnatha* Latreille 1804, *Glenognatha* Simon 1887 and *Pachygnatha* Sundevall 1823. The six trees conflict in the placement of *Leucauge* White 1841, which is

sister either to *Sancus* + tetragnathines (Fig. 17) or sister to *Meta* C.L. Koch 1836, *Metellina* Chamberlin & Ivie 1941 and *Chrysometa* Simon 1894, as well as in the position of *Epeirotypus* O. P.-Cambridge 1894 relative to the sheet-web builders. Successive weighting resulted in one stable topology after a single iteration, identical to one of the most parsimonious cladograms under equal weights (Fig. 17). Bremer support and bootstrap support values are mapped on this preferred phylogeny.

The diagnostic characters and synapomorphies (Fig. 18) of the genus *Sancus* (under DELTRAN optimization; see justification below) are the CBP apical denticles (61/1), the epigynal transverse bar (62/1) and the epigynal ventral depression (63/1). Another diagnostic character, lack of dorsal femoral trichobothria (7/1) serves as synapomorphy under ACCTRAN (Fig. 18). In addition, unambiguous synapomorphies of *Sancus* (homoplasious on the cladogram) are mesal cymbium

orientation (21/1) and procurved CBP (25/1) (see Character analysis).

#### DISCUSSION

Monotypic genera are problematic because they contain no grouping information and therefore are not phylogenetic hypotheses (Zujko-Miller 1999). Platnick (1976, 1977) also argued that monophyly cannot apply to monotypic genera. In some cases, taxonomists have no choice but to retain monotypic genera (e.g. Kuntner 2002), for example if the sister species or clade is unknown or unresolved. By synonymizing *Leucognatha* with *Sancus* we rid tetragnathid systematics of two monotypic genera.

**Alternative optimizations and synapomorphies.**—Delayed transformation (DELTRAN) optimizes three out of four diagnostic *Sancus* characters as synapomorphies for the genus (Fig. 18). The accelerated transformation alternative (ACCTTRAN) optimizes the CBP denticles (character 61) as a synapomorphy for *Leucauge* + (*Sancus* + tetragnathines) (Fig. 18). However, the CBP itself (character 25) is primitively absent at this node. Since the CBP denticles are an attribute of the CBP, any optimization in which the denticles arise before the process is illogical, an artifact resulting from the inapplicable coding of the CBP denticles (character 61) in *Leucauge* and tetragnathines, which lack the CBP. Since the presence of the CBP is an unambiguous synapomorphy of *Sancus*, the DELTRAN alternative is more reasonable, implying the evolution of the CBP denticles (along with the CBP) in the common ancestor of *Sancus*.

ACCTTRAN optimizes the two new epigynal characters (62, 63) as synapomorphies of *Sancus* + Tetragnathinae. However, tetragnathines are haplogyne, meaning they lack the epigynum (40/1) and fertilization ducts (41/1), both unambiguous synapomorphies of the clade (Fig. 18). Thus, for tetragnathines, the two new epigynal characters are inapplicable. The ACCTTRAN optimization implicitly assumes tetragnathine ancestor had the *Sancus* epigynal characters but lost them (along with the epigynum itself), an unwarranted presumption. In this case, DELTRAN is a simpler explanation of the data.

The presence of dorsal femoral trichobothria (character 7/0) served as a synapomorphy for *Leucauge* + tetragnathines in Hormiga et

al. (1995). In this analysis the optimization of this homoplasious character is ambiguous (Fig. 18). ACCTTRAN resolves the presence of trichobothria as a synapomorphy for *Leucauge* + (*Sancus* + tetragnathines) and the absence as a synapomorphy of *Sancus*. On the other hand, DELTRAN favors two separate origins (Fig. 18) and thus implies that trichobothria in *Leucauge* may not be homologous to the ones in tetragnathines.

**Phylogenetic placement with comments on tetragnathid relationships.**—This paper establishes the phylogenetic placement of *Sancus*, not new phylogenetic relationships of the tetragnathid genera. The preferred phylogeny (Fig. 17) agrees with the phylogeny found by Hormiga et al. (1995), and *Sancus* groups with tetragnathines. Of course, we basically re-ran the Hormiga et al. (1995) data, so such congruence is not surprising, even though we think some homology statements should be reassessed. We will present these new hypotheses in future papers on nephiline and metine systematics.

Three unambiguous synapomorphies support the group *Sancus* + Tetragnathinae: 1) long and finger-like paracymbium (Figs. 11–14); 2) presence of an anterior paracymbial apophysis (Figs. 13, 14); 3) spiraled reservoir course (homoplasious). One unambiguous but weak synapomorphy supports *Leucauge* + (*Sancus* + tetragnathines): posterior gut caeca (character 11 of Hormiga et al. 1995), but we did not score the feature for *Sancus* because specimens are too rare to dissect.

The tetragnathid phylogeny, as currently understood (Fig. 17), must be considered preliminary and interpreted cautiously. Hormiga et al. (1995) did not present branch support statistics, but most nodes are poorly supported (Fig. 17; Bremer = 1, bootstrap < 50%). Bootstrapping collapsed 11 out of 20 nodes and tetragnathid monophyly collapsed. Nephilinae, especially distal nephilines (*Clitaetra* (*Nephila* (*Herennia* + *Nephilengys*), and Tetragnathinae are well supported (also in Hormiga et al. 1995). On the other hand, current work disputes the placement of the nephiline clade as tetragnathids (Kuntner 2003; Kuntner 2005, 2006a & b) and some genera, traditionally classified as nephilines, have been transferred to Araneidae (Kuntner 2002; Kuntner & Hormiga 2002).

Wunderlich (1992:359) placed *Leucognatha*

(= *Sancus*) in Leucauginae, but did not provide synapomorphies for the subfamily. All *Leucauge* species possess characteristic rows of fourth femoral trichobothria (Levi 1980: figs. 50, 51, 67). Similar condition can be found in tetragnathid genera *Opadometa* Archer 1951, *Tylorida* Simon 1894, *Mesida* Kulczynski 1911 and *Orsinome* Thorell 1890 (none of them placed phylogenetically), but not in *Sancus*. Femoral trichobothria of tetragnathines, though present, are not in rows and may not be homologous to the *Leucauge* condition (Fig. 18; see above). We will test and discuss homology of femoral trichobothria in *Leucauge* and tetragnathines and possible monophyly of 'leucaugines' and 'metines' elsewhere.

**Behavior.**—*Sancus* behavior and web architecture are unknown. Our prediction based on the phylogenetic outcome is that *Sancus* builds orb webs with an open hub and few radii, which are more horizontal than vertical. *Leucauge* and most *Tetragnatha* species build such webs (e.g. Levi 1980; own data). *Sancus acoreensis* was collected adjacent to bodies of water (Wunderlich 1992), which is typical for *Tetragnatha*.

**Biogeography.**—*Sancus* is now known from the Azores in the Atlantic Ocean and two mountain peaks (Kilimanjaro and Mt. Kenya) in equatorial eastern Africa (Fig. 15). The two areas are more than 7,500 km apart, in very different climatic regimes, latitudes and elevations, and are habitat islands. The Azores are 1,370 km from Europe and 1,530 km from Africa. The type series of *S. bilineatus* says 3,000 m on Kilimanjaro; the other collection simply says Mt. Kenya. We are not aware of any other comparable taxon distribution.

This unusual distribution is probably an undersampling artifact. However, we tried but failed to find more *Sancus* material in African collections. *Sancus* (= *Leucognatha*) is apparently also absent from Madeira and the Canary Islands (Wunderlich 1992: 359; see also Fig. 15), which lie between the Azores and the mainland Africa; nor does the genus occur in the Mediterranean.

If not artifactual, the distribution might be explained either by extinction of *Sancus* in intervening Africa or dispersal and divergence into the two clearly diagnosable species we see today. An undiscovered African population of *S. acoreensis* might also exist and have

been introduced to the Azores. We expect more records of *Sancus* in the future from Africa, Macaronesia, and perhaps from the Mediterranean, and hope this paper will facilitate such discoveries.

#### ACKNOWLEDGMENTS

We thank Jonathan Coddington, Gustavo Hormiga, Jeremy Miller and Ingi Agnarsson for valuable help and comments to an early draft. Mark Harvey, Peter Cranston, Rudy Jocqué, Lara Lopardo and three anonymous reviewers also much improved our paper. Jörg Wunderlich kindly shared unpublished data and provided useful comments. Jeremy Miller helped with the distribution map illustrations. Torbjörn Kronestedt (SMNH) and Jörg Wunderlich kindly loaned or donated the specimens for this study. Further curatorial help came from Jonathan Coddington and Dana deRoche at USNM, Charles Griswold, Darrel Ubick and Diana Silva at CAS, Norman Platnick, Randy Mercurio and Lou Sorkin at AMNH, Jason Dunlop at ZMB, Rudy Jocqué at RMCA, Janet Beccaloni at BMNH and Christine Rollard at MNHN. This project was supported by U.S. National Science Foundation grants DEB-9712353 and DEB-0328644, and collection study grants from CAS and AMNH. Alvarez-Padilla has been supported by a doctoral fellowship from CONACYT (Consejo Nacional de Ciencia y Tecnología, México). We further acknowledge the financial and logistical support of the George Washington University and the Smithsonian Institution.

#### LITERATURE CITED

- Boeck, A. 1872. Nye Slaegter og Arter af Saltvands-Cpepoder. Forhandlinger i Videnskabs-Selskabet i Christiania 1872:35–60.
- Bonnet, P. 1958. Bibliographia Araneorum, Vol. 2, Part 4, (N-S). Toulouse, Les Frères Douladoure.
- Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* 42:795–803.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10:295–304.
- Brignoli, P.M. 1983. A Catalogue of the Araneae Described Between 1940 and 1981. Manchester, Manchester University Press in association with The British Arachnological Society.
- Coddington, J.A. 1983. A temporary slide mount allowing precise manipulation of small structures. Pp. 291–292. *In* Taxonomy, Biology and Ecology of Araneae and Myriapoda (O. Kraus,

- ed.). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg, New Series 26.
- Dippenaar-Schoeman, A.S. & R. Jocqué. 1997. African Spiders—An Identification Manual. Pretoria, ARC—Plant Protection Research Institute.
- Fitch, W.M. 1971. Towards defining the course of evolution: Minimal change for a specific tree topology. *Systematic Zoology* 20:406–416.
- Goloboff, P.A. 1993. NONA version 2.0. Available at <http://www.cladistics.com/>.
- Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharff. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society* 123(1):1–99.
- Holm, C. 1979. A taxonomic study of European and East African species of the genera *Pelecopsis* and *Trichopterna* (Araneae, Linyphiidae), with descriptions of a new genus and two new species of *Pelecopsis* from Kenya. *Zoologica Scripta* 8: 255–278.
- Hormiga, G. 1994. A revision and cladistic analysis of the spider family Pimoidae (Araneoidea: Araneae). *Smithsonian Contributions to Zoology* 549:1–104.
- Hormiga, G. 2002. *Orsonwelles*, a new genus of giant linyphiid spiders (Araneae) from the Hawaiian Islands. *Invertebrate Systematics* 16:369–448.
- Hormiga, G., W.G. Eberhard & J.A. Coddington. 1995. Web-construction behavior in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). *Australian Journal of Zoology* 43:313–364.
- Kuntner, M. 2002. The placement of *Perilla* (Araneae, Araneidae) with comments on araneid phylogeny. *Journal of Arachnology* 30:281–287.
- Kuntner, M. 2003. The systematics of nephiline spiders (Araneae, Tetragnathidae). *American Arachnology* 66:9.
- Kuntner, M. 2005. A revision of *Herennia* (Araneae: Nephilidae: Nephilinae), the Australasian ‘coin spiders’. *Invertebrate Systematics* 19(5): 391–436.
- Kuntner, M. 2006a. Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). *Zoologica Scripta* 35(1): 19–62.
- Kuntner, M. 2006b. A monograph of *Nephilengys*, the pantropical ‘hermit spiders’ (Araneae, Nephilidae, Nephilinae). *Systematic Entomology* in press.
- Kuntner, M. & G. Hormiga. 2002. The African spiders genus *Singafrotypa* (Araneae, Araneidae). *Journal of Arachnology* 30:129–139.
- Levi, H.W. 1980. The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 149:1–75.
- Nixon, K. 2002. Winclada version 1.00.08. Available at <http://www.cladistics.com/>.
- Petrunkovitch, A. 1928. *Systema Araneorum*. Transactions of the Connecticut Academy of Arts and Sciences 29:1–270.
- Platnick, N.I. 1976. Are monotypic genera possible? *Systematic Zoology* 25:189–199.
- Platnick, N.I. 1977. Monotypy and the origin of higher taxa: a reply to W.O. Wiley. *Systematic Zoology* 26:355–357.
- Platnick, N.I. 2004. The World Spider Catalog, Version 4.5. The American Museum of Natural History. Available at <http://research.amnh.org/entomology/spiders/catalog>.
- Roewer, C.F. 1942. Katalog der Araneae von 1758 bis 1940, bzw. 1954. Vol. 1. Bremen, Kommissions-Verlag von “Natura”, Paul Budy.
- Simon, E. 1894. Histoire naturelle des araignées. Paris 1(3):489–760.
- Swofford, D.L. 2002. PAUP\*. Phylogenetic Analysis Using Parsimony (\*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Tullgren, A. 1910. Araneae. Wissenschaftliche Ergebnisse der Schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaistepfen Deutsch-Ostafrikas 1905–1906 unter Leitung von Prof. Dr. Yngve Sjöstedt. Swedish Academy of Sciences, Stockholm, 20(6):85–172.
- Wunderlich, J. 1992. Die Spinnen-Fauna der Makaronesischen Inseln: Taxonomie, Ökologie, Biogeographie und Evolution. Beiträge zur Araneologie 1:1–619.
- Zujko-Miller, J. 1999. On the phylogenetic relationships of *Sisicottus hibernus* (Araneae, Linyphiidae, Erigoninae). *Journal of Arachnology* 27: 44–52.

*Manuscript received 11 May 2004, revised 16 July 2004.*