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A REDESCRIPTION OF *PORRHOMMA CAVERNICOLA* KEYSERLING (ARANEAE, LINYPHIIDAE) WITH NOTES ON APPALACHIAN TROGLOBITES

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ABSTRACT. The Appalachian troglobite *Porrhomma cavernicola* (Keyserling 1886) is redescribed. *Porrhomma emertoni* Roewer 1942 is a junior synonym (new synonymy). An unusual stridulatory organ with the plectrum on trochanter II and the striae on coxa I is found in both sexes of this species. *Porrhomma cavernicola* is widespread in Appalachian caves. By contrast, Appalachian *Nesticus* (Nesticidae) troglobites tend to be highly endemic. This despite the fact that both groups of spiders are web-builders that may be found in the same caves. *Porrhomma cavernicola* is added to a previous phylogenetic analysis of linyphiid spiders. Implications of this analysis for the phylogenetic structure of linyphiid spiders is discussed.

Keywords: Dispersal, phylogeny, stridulatory organ, *Nesticus*, Nesticidae

There is a continuous gradation between epigean and troglobitic organisms. While a variety of spiders are known from cave entrances or can be found both in and out of caves, true troglobites complete their entire life cycle in caves. In the Appalachian region, true troglobites belong to the Linyphiidae, Nesticidae, Dictynidae and Leptonetidae (Barr 1961; Holsinger & Culver 1988; Gertsch 1992; Peck 1998). Dictynid and leptonetid troglobites in Appalachia are understudied and will not be discussed further here (see Miller 2005).

Porrhomma cavernicola (Keyserling 1886) is one of two linyphiid troglobites widespread and often syntopic in Appalachian caves. The other widespread linyphiid troglobite is *Phanetta subterranea* (Emerton 1875) (Fig. 1). *Anthrobia* are also widespread in Appalachian caves, although Miller (2005) has concluded that there are at least two troglobitic *Anthrobia* species instead of the one species previously recognized. Some other linyphiid troglobites have more restricted distributions (e.g., some *Islandiana* species, Holsinger & Culver 1988; Gertsch 1992; Peck 1998; also some undescribed species, N. Dupérré, pers. comm.). Multiple linyphiid troglobite species can often be found in the same cave. By contrast, troglobitic species of *Nesticus* (Nesticidae) in Appalachian caves are never widespread, highly endemic, and rarely syntopic (Fig. 1; Gertsch 1984; Coyle & McGarity 1991; Hedin 1997b; Reeves 2000; Hedin & Dellinger 2005). About eight Appalachian *Nesticus* species appear to be troglobites (Gertsch 1984, 1992; Hedin 1997a; Hedin & Dellinger 2005). In both *Nesticus* (Hedin 1997a, b) and linyphiids, troglobitism seems to have occurred independently multiple times.

Widespread troglobites are the exception to the rule. Troglobites cannot normally survive long under surface conditions so dispersal between cave-islands across epigean seas must be rare (Barr 1967; Culver 1970, 1971, 1982; Barr & Holsinger 1985; Holsinger & Culver 1988). Thus widespread troglobites must either be a syndrome of multiple forms erroneously lumped into a single species by taxonomists, or genetically isolated populations that have not diverged because of insufficient time or low rates of change, or there must be some mechanism allowing gene flow between caves. Examination of specimens from across the range of *Porrhomma cavernicola* revealed no clear pattern of geographical variation that

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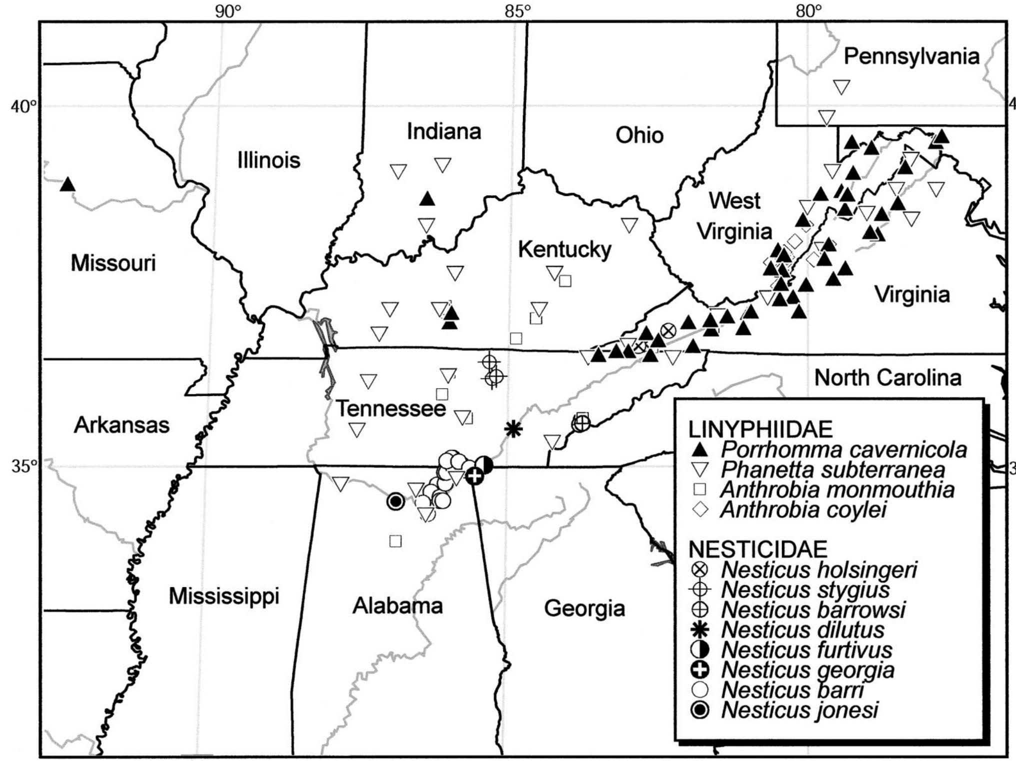


Figure 1.—Map showing distribution of nesticid and selected linyphiid troglobites in Appalachian caves. Records of *Phanetta subterranea* from Millidge (1984); of *Anthrobia monmouthia* and *Anthrobia coylei* from Miller (2005); of *Nesticus* species from Gertsch (1984) and Hedin (1997a, 1997b).

would suggest cryptic species (Figs. 2–4). This contrasts with the conclusion reached concerning troglobitic *Anthrobia*. *Anthrobia monmouthia* was previously considered a widespread Appalachian troglobite, but new work has provided diagnoses and descriptions for two distinct species that were previously confused under this name (Miller 2005). Efforts are underway to study the population genetics of widespread linyphiid troglobites in Appalachia to evaluate gene flow among caves.

METHODS

Specimens were examined using a Leica MZ 16 dissecting microscope. Most illustrations of the genitalia were made using an Olympus BH-2 compound microscope fitted with a camera lucida. Specimens were temporarily cleared in methyl salicylate (Holm 1979), then positioned for illustration on a temporary slide using the method described in Coddington (1983). The illustration of the epigynum in ventral view was based on photographs taken using a Nikon DXM 1200F digital camera mounted on a Leica MZ 16. The photograph of the cleared epigynum was taken using the digital camera mounted on an Ortholux II compound microscope; multiple images were combined using Auto-Montage by Syncroscopy (version 4.01). SEM images were taken using the AMRAY 1800 at the National Museum of Natural History Scanning Electron Microscope Facility.

All measurements are in millimeters and were taken using a reticle mounted in a Leica MZ APO dissecting microscope. The position of the first metatarsal trichobothrium (TmI) is expressed as the ratio of the distance between the proximal margin of the metatarsus and the root of the trichobothrium divided by the total length of the metatarsus (Denis 1949; Locket & Millidge 1953).

Material examined.—When multiple consecutive records in the material examined section were from the same locality, the locality data after the first record is given in brackets as [same locality]. When data labels did not include geographic coordinates, I attempted to determine the approximate location using maps, gazetteers, and other literature. Once the location was inferred, the coordinates were included in [square brackets]; coordinates taken directly from the data label are given in (parentheses). When no coordinates could be determined for any cave within a county, a dot near the geographic center of the county was included in the map (Fig. 1). In most cases, coordinates will not be precise enough that readers will be able to locate caves without additional information. The map was created using ArcView version 8.3.

Phylogenetic analysis.—*Porrhomma cavernicola* was coded into the phylogenetic data matrix of Miller (2005); no new characters were added to the analysis. The expanded analysis consists of 87 taxa coded for 176 characters, 172 of which are phylogenetically informative. The majority of characters concern the male genitalia, somatic morphology, and female genitalia; a few characters concern behavior and web architecture. See (Miller & Hormiga 2004) for descriptions of characters and character states. *Porrhomma cavernicola* was coded as follows: 0000001000 0401010–01 1001000010 0000000101 1000000001 1100100000 0–00000–0 0012001000 0–00000001 0100100100 000000000? 2100011 000 0041011111 3211111111 1111100000 000?000–00–201110011? ?????. Analysis was conducted using heuristic searches in PAUP* (1000 replicates of random taxon addition; Swofford 2001). All characters were treated as unordered and equally weighted.

Abbreviations.—The following anatomical abbreviations are used in the text and figures: A = atrium; AC = aciniform gland spigot; AG = aggregate gland spigots; ALE = anterior lateral eye; AME = anterior median eye; ARP = anterior radical process; CD = copulatory duct; CL = column; DP = dorsal plate of epigynum; DSA = distal suprategular apophysis; E = embolus; EM = embolic membrane; F = fundus; FE = femur; FL = flagelliform gland spigot; FD = fertilization duct; MT = metatarsus; PA = patella; PC = paracymbium; PLE = posterior lateral eye; PME = posterior median eye; PT = protegulum; R = radix; S = spermatheca; SPT = suprategulum; ST = subtegulum; T = tegulum; TA = tarsus; TI = tibia; TLL = total leg length; TmI = position of first metatarsal trichobothrium; TmIV = fourth metatarsal trichobothrium; TP = tailpiece of radix; VP = ventral plate of epigynum. Institutional abbreviations are given in the Acknowledgments.

TAXONOMY

Family Linyphiidae Blackwall 1859
Genus *Porrhomma* Simon 1884

Porrhomma Simon 1884: 360. Type species *Linyphia proserpina* Simon 1873 (=*Erigone convexa* Westring 1851, synonymy in Holm 1944: 130, 133) by subsequent designation (Simon 1894: 701).

Opistoxys Simon, 1884: 373. Type species *Opistoxys acuta* Simon 1884 (=*Linyphia microphthalma* O. Pickard-Cambridge 1871, synonymy in Thaler 1975: 142) by monotypy. Synonymy in Thaler 1975: 142.

Remarks.—The Holarctic genus *Porrhomma* consists of 31 species plus one subspecies (Platnick 2004). The species of the genus tend to be quite homogeneous, but within species, the genitalia tend to exhibit a high degree of variation. Species range in total length from about 1.2–3.2. Most species are epigean, found mostly in cool, mesic habitats including forests, grasslands, and under stones. Some species are troglophilic [e.g., *P. convexum* (Westring 1861) and *P. egeria* Simon 1884], while others are troglobites [e.g., *P. cavernicola* and *P. rosenhaueri* (L. Koch 1872)].

Porrhomma cavernicola (Keyserling 1886)
Figs. 1–26

Linyphia incerta Emerton 1875:280, figs. 13–21 (♂, ♀); Packard 1875:275; Packard 1888:57; MacCook 1890:292, figs. 284–285; Simon 1894:690.

Willibaldia incerta (Emerton): Keyserling 1886: 123; Marx 1890:531; Banks 1910:32.

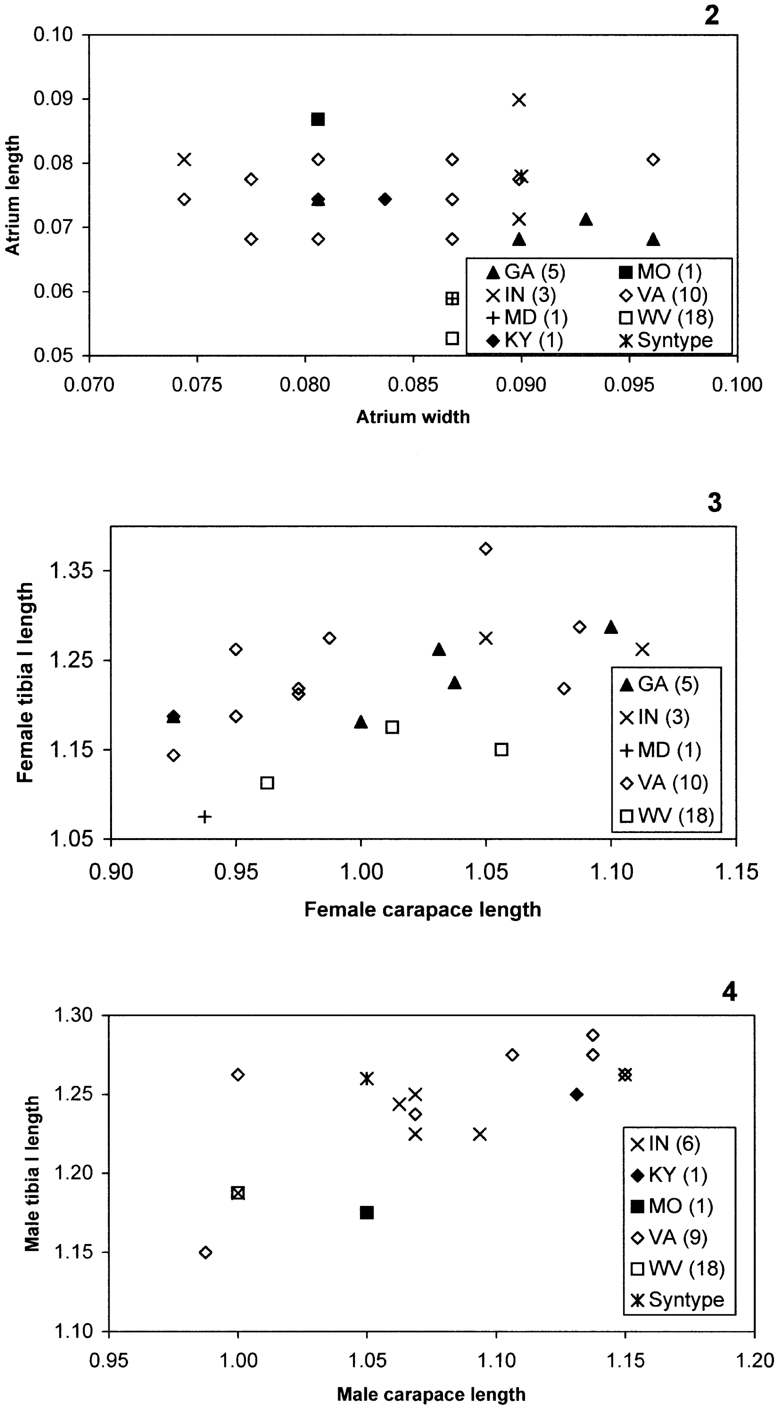
Willibaldia cavernicola Keyserling 1886:123–124, pl. 15, fig. 204 (♀); Packard 1888:58; Marx 1890: 531; Comstock 1903:32; Banks 1907:739, Banks 1910:32; Comstock 1913:383; Comstock 1948: 397; Bonnet 1959:4721.

Taranucnus cavernicola (Keyserling): Simon 1894: 690.

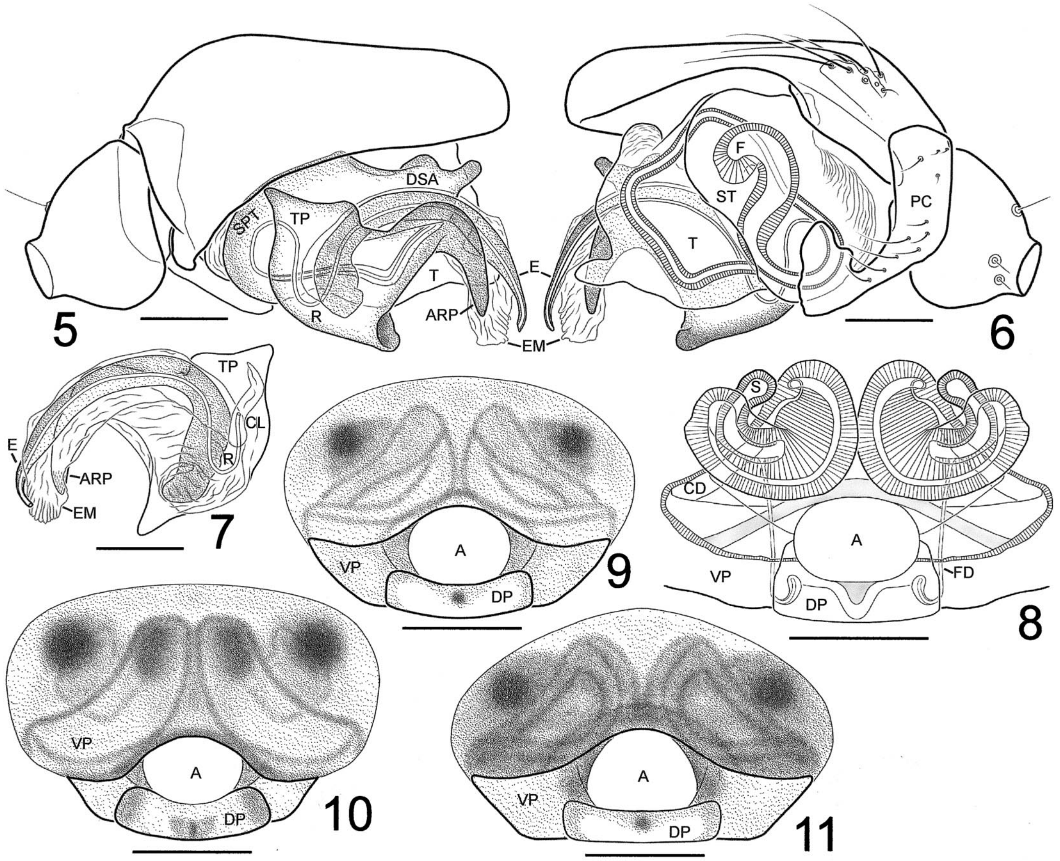
Troglohyphantes cavernicola (Keyserling): Simon 1894:706; Crosby 1905:368, figs. 20–22 (♂); McIndoo 1910:304; McIndoo 1911a:183; McIndoo 1911b:391.

Troglohyphantes incertus (Emerton): Comstock 1903:32; Comstock 1913:383; Petrunkevitch 1911:272.

Troglohyphantes cavernicolus (Keyserling): Com-



Figures 2–4.—Morphometric variation of selected features in *Porrhomma cavernicola*. Individuals grouped by state with sample size in parentheses. The syntype specimens of *Willibaldia cavernicola* are indicated by an asterisk symbol. 2. length and width of the atrium, female epigynum; 3. tibia I length and carapace length in female; 4. tibia I length and carapace length in male.



Figures 5–11.—*Porrhomma cavernicola* (Keyserling). 5–7. left male palp; 8–11. epigynum. 5. prolateral view; 6. retrolateral view; 7. embolic division, mesal view; 8. dorsal view; 9–11. ventral view. 5–9. from Sam Six Cave, Wythe County, Virginia; 10. from McFerrin Breakdown Cave, Greenbrier County, West Virginia; 11. from El Rod Cave, Orange County, Indiana. Scale bars = 0.1 mm. See text for abbreviations.

stock 1903:32; Comstock 1913:383; Petrunkevitch 1911:272; Elliott 1932:425.
Willibaldi cavernicola (Keyserling): Banta 1907:62.
Porrhomma incerta (Emerton): Berland 1931:384.
Porrhomma cavernicola (Keyserling): Roewer 1942:603; Platnick 2004.
Porrhomma emertoni Roewer 1942:603 (replacement name for *Linyphia incerta* Emerton 1875, preoccupied by *Linyphia incerta* Walckenaer 1842, nomen dubium, see van Helsdingen 1972); Platnick 2004. NEW SYNONYMY.
Porrhomma incertum (Emerton): Bonnet 1958: 3756.

Justification of Synonymy.—Berland (1931) noted that the two nominal taxa appear to differ very little, but he did not synonymize them. After examination of the types and other specimens, I found no morphological evidence to maintain two diagnosable species of troglobitic *Porrhomma* in the Appalachian region. Selected morphometric characteristics failed to show any regional pattern that might indicate multiple species (Figs. 2–4). A similar approach did reveal the presence of multiple species in troglobitic *Anthrobia* (Miller 2005).

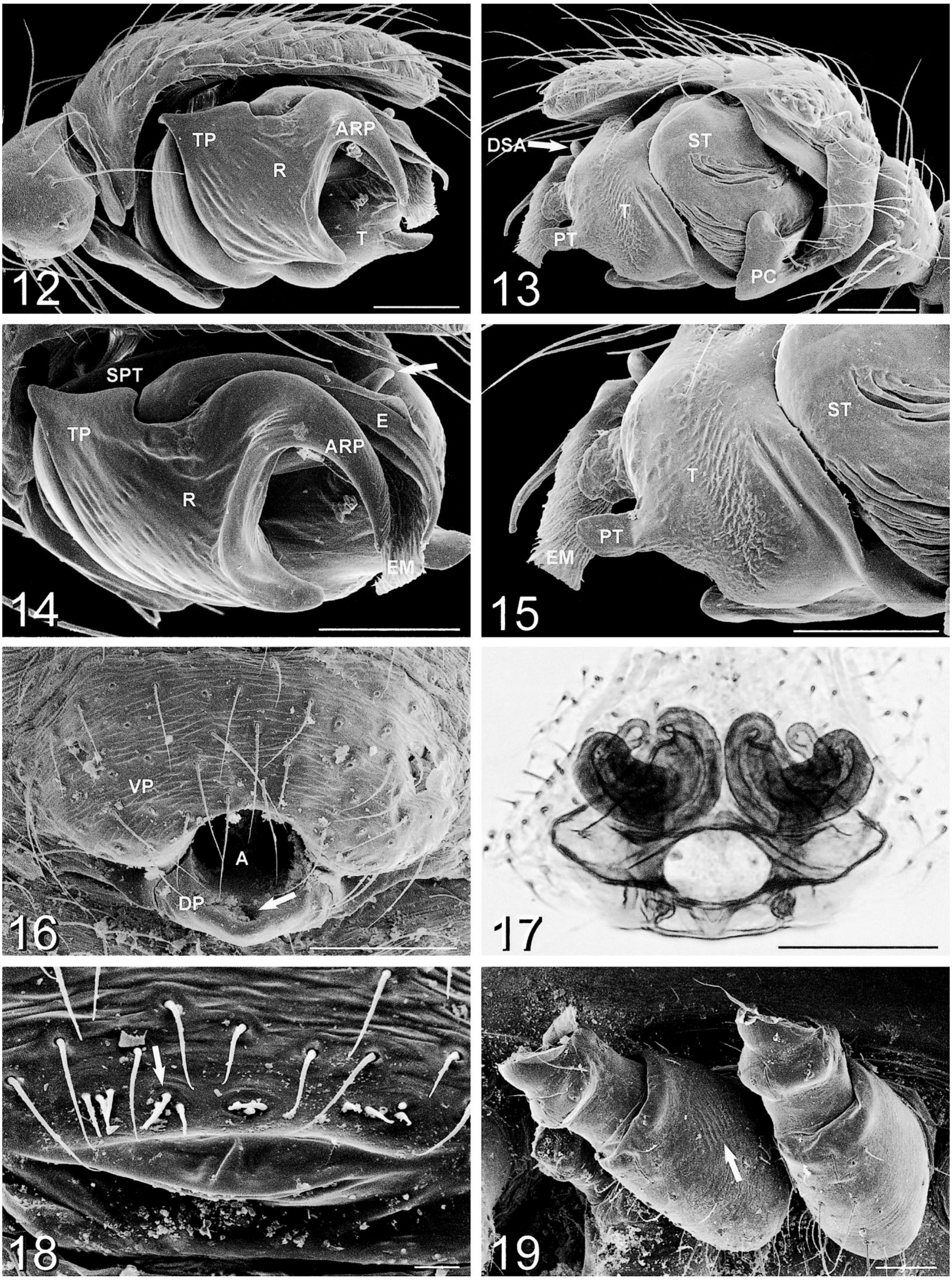
Nomenclature.—*Linyphia incerta* Emerton 1875 is a primary homonym of *Linyphia incerta* Walckenaer 1842 and is therefore permanently invalid (International Commission on Zoological Nomenclature 1999, Article 57.2). Roewer (1942) proposed *Porrhomma emertoni* Roewer 1942 as a replacement name for *L. incerta*. *Willibaldia cavernicola* Keyserling 1886 has priority over *P. emertoni*.

Types.—UNITED STATES: *Kentucky:* Barren County, Reynolds Cave (BMNH, 1890.7.1.8242–8243, syntypes of *Willibaldia cavernicola*, examined), 1 ♂, 1 ♀. General condition degraded; male abdomen missing, as are most legs for both specimens; female prosoma and abdomen disarticulated. *Male:* Carapace 1.05 long, 0.76 wide, tibia I 1.26. *Female:* Carapace 1.16 long, 0.78 wide, atrium 0.078 long, 0.090 wide.

Virginia: Augusta County, Fountain Cave [38°10′N, 78°55′W], Packard (MCZ, syntypes of *Linyphia incerta*, examined), 2 ♂, 4 ♀, 5 juveniles.

Additional Material Examined.—UNITED STATES: *Georgia:* Bartow County, Kingston Saltpeter Cave (34°12′N, 84°54′W), 2 June 1999, W. Reeves (USNM), 5 ♀. *Indiana:* Lawrence County, JJ's Sister Cave (38°45′N, 86°36′W), 26 August 2004, J. Miller (USNM), 1 ♂; Orange County, El Rod Cave (38°37′N, 86°31′W), 26 August 2004, P. Paquin, J. Miller, J. Lewis, N. Dupérré (USNM), 4 ♂, 1 ♀, 3 juveniles; [same locality], inside cave, shallow cave, hand collecting, P. Paquin, N. Dupérré (USNM, PP-2304), 2 ♀, juveniles. *Kentucky:* Carter County, Carter Cave, A Cave [38°22′N 83°07′W], Packard (MCZ), 1 ♂, 2 ♀. *Maryland:* Garrett County, Crabtree Cave, 24 September 1987, pool surface, right passage, D. Feller (USNM, 51B), 1 ♀; Washington County, Fairview Cave, 30 September 1988, pool surface, mudslide area, D. Feller (USNM, 131C), 1 ♀. *Missouri:* Boone County, Rocheport Cave, 3 miles below Rocheport [38°55′N, 92°30′W], 23 July 1905, C.R. Crosby (MCZ), 1 ♂, 1 ♀. *Virginia:* Augusta County, Fountain Cave [38°10′N, 78°55′W], (MCZ), 1 ♂; Page County, Lurray [sic, Luray] Cave [38°39′N, 78°29′W], Kochele (USNM, 187), 2 ♀ [in two vials]; Page County, Luray Cave [38°39′N, 78°29′W], R.V. Chamberlin (MCZ, 59645), 1 ♂, 2 ♀; Montgomery County, Aunt Nelli's hole (37°12′N, 80°22′W), 5 September 2004, P. Paquin, J. Miller, N. Dupérré, R. Storey (USNM), 1 ♂, 1 juvenile; [same locality], 5 September 2004, inside cave, hand collecting, P. Paquin, N. Dupérré (USNM, PP-4304), 1 ♀; Russell County, Cartop Cave, 26 November 1999, D. Hubbard (USNM), 3 ♂, 2 ♀, 3 juveniles; Russell County, Maggie Baker Cave, 17 September 1997, D. Hubbard (USNM), 3 ♀; Scott County, Abram's Cave, 15 December 1999, D. Hubbard (USNM), 1 ♂; Scott County, Little Duck Cave, 28 November 1997, D. Hubbard (USNM), 2 ♂, 1 ♀; Scott County, Queens Cave, 15 April 1997, D. Hubbard (USNM), 1 ♀; Washington County, Robinson Cave, 25 February 1997, D. Hubbard (USNM), 1 ♂; Wythe County, Sam Six Cave, 25 November 1998, D. Hubbard (USNM), 1 ♂, 2 ♀, 3 juveniles. *West Virginia:* Greenbrier County, McFerrin Breakdown Cave, 22 August 2004, visual, E. Saugstad, K. Schneider (USNM), 1 ♀; Mineral County, High Rock Fissure Cave, 30 October 1988, woodrat midden, rope drop, D. Feller (USNM, 133B), 1 ♂; Monroe County, Steeles Cave, 11 June 2004, visual (USNM), 1 ♂, 2 ♀. Two additional vials had no locality data: 1 ♂, 1 ♀, Banks (MCZ, 57184, 1753); 1 ♀, Banks (MCZ, 59646).

Additional Records.—The following records were compiled from literature sources (McIndoo 1910; Holsinger et al. 1976; Holsinger & Culver 1988). UNITED STATES: *Indiana:* Lawrence County, Shawnee Cave [now called Donaldson Cave], 3 miles E Mitchell. *Tennessee:* Claiborne County: Jennings Cave [36°33′N, 83°30′W]; Hawkins County: Sensabaugh Saltpeter Cave [36°34′N, 82°39′W]. *Virginia:* Augusta County: Glade Cave, Madisons Saltpeter Cave; Bath County: Clark's Cave [38°5′N, 79°39′W], Crossroads Cave, Porters Cave, Witheros Cave, Banes Spring Cave, Coon Cave; Craig County: New Castle Murder Hole Cave, Rufe Caldwell Cave; Frederick County: Beans Cave [39°9′N, 78°21′W]; Giles County: Clover Hollow Cave [37°19′N, 80°28′W]; Lee County: Unthands Cave, Fisher Cave; Page County: Luray Caverns [38°39′N, 78°29′W]; Ruffners Cave No. 1; Roanoke County: Dixie Caverns [37°9′N, 80°9′W]; Rockbridge County: Bell Cave [37°45′N, 79°22′W], Buck Hill Cave [37°36′N, 79°34′W]; Rockingham County: Three-D Maze Cave [38°30′N, 78°45′W]; Tazewell County: Gully Cave [37°2′N, 81°38′W], Lawson Cave [37°5′N, 81°21′W]; Wise County: Parsons Cave [36°51′N, 82°42′W]. *West Virginia:* Berkeley County: Whitings Neck Cave [39°30′N, 77°50′W]; Grant County: Klines Gap Cave [39°4′N, 79°14′W]; Greenbrier County: Bransfords Cave [38°0′N, 80°30′W], Higginbothams Cave [37°56′N, 80°24′W], Organ Cave [37°43′N, 80°26′W], Pollock Cave [37°45′N, 80°37′W], Pollock Saltpeter Cave; Monroe County: Fulton Cave [37°32′N, 80°27′W]; Pendleton County: Moyers Cave [38°34′N,



Figures 12–19.—*Porrhomma cavernicola* (Keyserling); 12–16, 18, 19. scanning electron micrographs; 12. photograph. 12–15. left male palp; 16, 17. epigynum; 18. epiandrous region of male; 19. coxa, trochanter I and II of female. 12. prolateral view; 13. retrolateral view; 14. embolic division, arrow indicates DSA; 15. detail of tegulum; 16. ventral view, arrow indicates socket in dorsal plate; 17. dorsal view, cleared; 18. arrow indicates epiandrous gland spigots; 19. arrows indicate striae on coxa I. 12–15. from High Rock Fissure Cave, Mineral County, West Virginia; 16, 19. from Fairview Cave, Washington County, Maryland; 17. from Cartop Cave, Russell County, Virginia; 18. from Sam Six Cave, Wythe County, Virginia. Scale bars = 0.01 mm (Fig. 18); 0.1 mm (Figs. 12–17, 19). See text for abbreviations.

79°22′W], Mystic Cave [38°49′N, 79°26′W], Schoolhouse Cave [38°47′N, 79°47′W], Seneca Caverns [38°47′N, 79°21′W], Stratosphere Balloon Cave [38°46′N, 79°20′W]; Pocahontas County: Sharps Cave [38°25′N, 80°5′W].

Diagnosis.—Troglobite distinguished from other *Porrhomma* species in North America by the extreme reduction of the eyes (Figs. 20–22). Note that *P. roserhaueri* L. Koch 1872, a cave associated species from Europe and Russia, also has reduced eyes (Locket & Millidge 1953, Wiehle, 1956, Roberts 1993, Platnick 2004). Males of *P. cavernicola* have the ARP much thicker and more ventrally-directed compared to *P. rosenhaueri* (see Roberts 1993, fig. 59E).

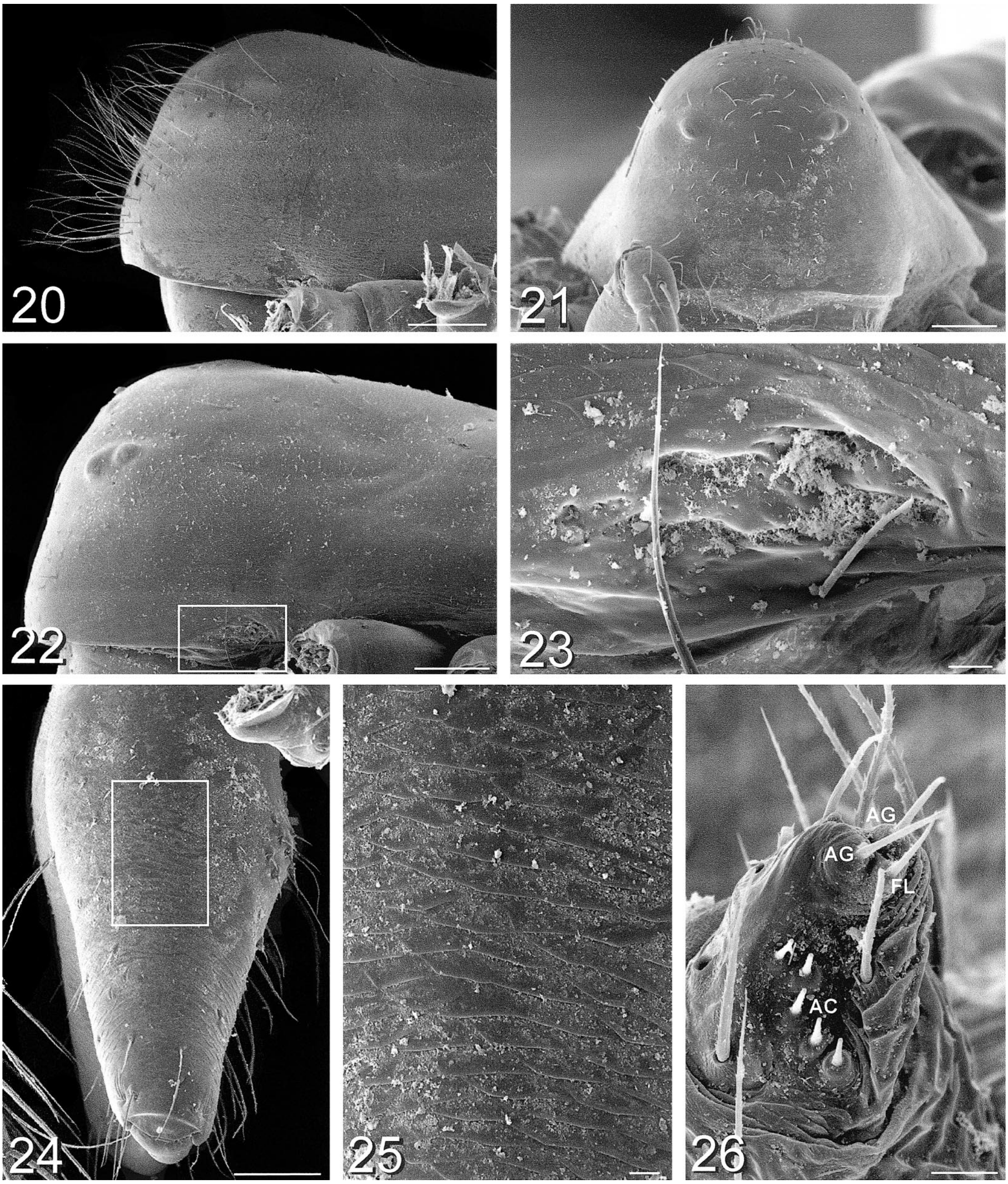
Description.—*Male (from Sam Six Cave, Wythe County, Virginia):* Total length 2.43. Carapace 1.19 long, 0.85 wide, orange, squamate to reticulate texture. Abdomen white. Eyes minute, laterals separated (see variation, below). Hairs on clypeus and ocular region relatively long (Fig. 20). Sternum 0.58 long, 0.58 wide, light orange. Coxa I with stridulatory striae on posterior face (as in Fig. 19). Coxa IV separation 0.93 times their width. Chelicerae orange, with three promarginal teeth, four retromarginal teeth; stridulatory striae scale-like (as in Figs. 24, 25). Sulcus present on margin of carapace posterior to chelicerae (as in Fig. 23). Legs orange, tibia I 12.25 times longer than thick; TmI 0.43. Leg I: FE 1.31, PA 0.29, TI 1.23, MT 1.10, TA 0.70, TLL 4.63; leg II: FE 1.23, PA 0.29, TI 1.13, MT 1.10, TA 0.68, TLL 4.63; leg III: FE 1.11, PA 0.25, TI 0.90, MT 0.86, TA 0.56, TLL 3.69; leg IV: FE 1.30, PA 0.28, TI 1.29, MT 1.13, TA 0.68, TLL 4.66. Epiandrous gland spigots present (Fig. 18). Anterior lateral spinnerets with five aciniform, flagelliform, and two aggregate gland spigots (Fig. 26); posterior median spinnerets with minor ampullate, two aciniform gland spigots. Palpal tibia with one prolateral, two retrolateral trichobothria (Fig. 6); tibial apophysis absent. Retrobasal region of cymbium with short apophysis bearing long setae and glabrous region along margin (Fig. 13). Paracymbium hook-like, proximal part clothed with macrosetae (Fig. 13). Subtegulum ectal to tegulum. Retrolateral part of tegulum partially covered in fine ridges (Fig. 15). Protegulum plus one other distal apophysis of the tegulum present (Fig. 15). Suprategulum continuous with tegulum, distal suprategular apophysis finger-like, projecting distally (Figs. 5, 14). Embolic division a plate-like radix with a short, posterior-projecting tailpiece and a long curved anterior radical process (Fig. 12). Basal part of embolus broadly articulated to radix by a membrane (Fig. 7); distal part of embolus partially wrapped by embolic membrane, which is covered in fine papillae (Fig. 14).

Female (same locality as male): Total length 2.55. Carapace 1.13 long, 0.79 wide, orange, squamate to reticulate texture. Abdomen white. Eyes minute, laterals separated (see variation, below). Hairs on clypeus and ocular region not as long as in male (Figs. 21, 22). Sternum 0.54 long, 0.55 wide, orange. Coxa I with stridulatory striae on posterior face (Fig. 19). Coxa IV separation 1.00 times their width. Chelicerae orange, with three promarginal teeth, four retromarginal teeth; stridulatory striae scale-like (Figs. 24, 25). Sulcus present on margin of carapace posterior to chelicerae (Figs. 22, 23). Legs orange, tibia I 12.13 times longer than thick; TmI 0.44. Palpal tibia with one prolateral, two retrolateral trichobothria; palpal tarsus with two dorsomesal, two dorsoectal macroseta, four ventromesal, two ventroectal macrosetae, claw absent. Leg I: FE 1.29, PA 0.29, TI 1.21, MT 1.05, TA 0.46, TLL 4.51; leg II: Fe 1.26, PA 0.29, TI 1.13, MT 0.99, TA 0.64, TLL 4.30; leg III: FE 1.09, PA 0.28, TI 0.86, MT 0.81, TA 0.54, TLL 3.58; leg IV: FE 1.31, PA 0.26, TI 1.28, MT 1.10, TA 0.66, TLL 4.61. Epigynum with deep circular atrium (Figs. 9–11, 16). Dorsal plate with socket (Fig. 16). Spermathecae crescent-shaped (Figs. 8, 17). Fertilization ducts arise from posterior part of spermathecae, long, straight, recurved terminally (Fig. 8). Copulatory ducts follow complex path, heavily sclerotized proximally, wider and less sclerotized close to atrium (Fig. 8).

Chaetotaxy: Femur I with one or two dorsal, two prolateral macrosetae; femur II with one or two dorsal macroseta. Tibia I and II with two dorsal, one prolateral, one retrolateral macrosetae; tibia III and IV with two dorsal macrosetae. TmIV absent.

Tracheae: Haplotracheate, four unbranched trunks confined to abdomen.

Variation.—Some or all eyes may be absent; eye loss not always bilaterally symmetrical. Variation in epigynum illustrated in Figs 2, 9–11.



Figures 20–26.—*Porrhomma cavernicola* (Keyserling); scanning electron micrographs. 20. male prosoma; 21–23. female prosoma, box in 22 defines area of image 23; 24, 25. female chelicera, box in 23 defines area of image 25; 26. anterior lateral spinneret of male. 20, 22. lateral view; 21. anterior view; 23. sulcus; 24. lateral; 25. detail. 20, 26 from Cartop Cave, Russell County, Virginia; 21, 24, 25. from Queens Cave, Scott County, Virginia; 22, 23. from Fairview Cave, Washington County, Maryland. Scale bars = 0.01 mm (Figs. 23, 25, 26); 0.1 mm (Figs. 20–22, 24). See text for abbreviations.

Natural History.—McIndoo (1910) reported that *P. cavernicola* ''. . . are found only in total darkness, where the atmosphere is saturated. . . '' McIndoo described the web as a sheet, slightly curved downward with the spider on the underside.

Distribution.—Known from caves in Georgia, Indiana, Kentucky, Maryland, Missouri, Tennessee, Virginia, and West Virginia (Fig. 1).

DISCUSSION

Phylogenetic Relationships and Character Evolution.—Analysis of the expanded data matrix (Miller 2005 plus *P. cavernicola*; see also Miller & Hormiga 2004) yielded a single most parsimonious tree (L = 931, CI = 0.23, RI = 0.59; with four autapomorphic characters excluded: L = 927, CI = 0.23; Fig. 27). The topology is identical to that found in Miller (2005) with *Porrhomma* placed sister to a clade consisting of Mynogleninae plus Erigoninae. *Porrhomma* has traditionally been placed in the Linyphiinae (e.g., Merrett 1963; Millidge 1977; Brignoli 1983). *Porrhomma* does not form a monophyletic group with the linyphiines included in the analysis (Fig. 27). Admittedly, this analysis suffers from sparse taxon sampling among non-erigonine linyphiids so the conclusions presented here must be considered preliminary. More robust taxon sampling from a variety of non-erigonine linyphiids plus the addition of molecular sequence data is called for.

Miller & Hormiga (2004) added taxa and characters to a previous analysis of erigonine relationships (Hormiga 2000). Considering only taxa common to both studies, relationships changed dramatically from one study to the next. Miller & Hormiga (2004) investigated whether the addition of taxa, characters, or both were primarily responsible for the changes in the tree. They concluded that most of the changes were due to the addition and modification of characters, not the addition of taxa. Miller (2005) added four taxa from the genus *Anthrobia* to the Miller & Hormiga (2004) matrix. Consistent with the conclusions of Miller & Hormiga (2004) about the relative insensitivity of their topological results to the addition of taxa, relationships of taxa included in both analyses were identical. For this study, one additional taxon has been added. Again, relationships among previously-included taxa are unchanged.

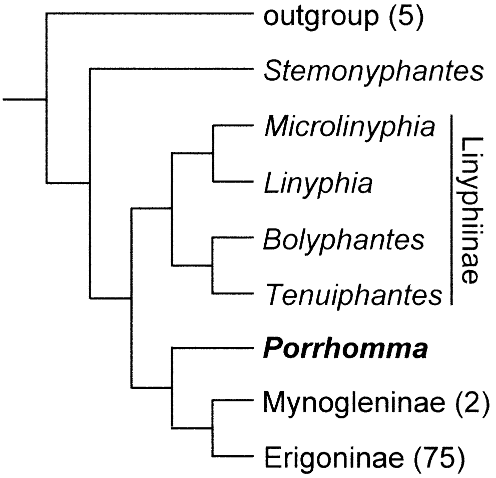


Figure 27.—Summary of phylogenetic analysis results showing the position of *Porrhomma*. Labels representing multiple terminals have the number of taxa in parentheses. See Miller (2005) for a more detailed tree figure (without *Porrhomma*); see Miller & Hormiga (2004) for characters and states.

Hormiga (1999) reported the presence of lateral sulci on the margin of the prosoma in both males and females in *Porrhomma* (Figs. 22, 23), as well as *Bathyphantes* Menge 1866, *Diplostyla* Emerton 1882, *Kaestneria* Wiehle 1956, *Pacifiphantes* Eskov & Marusik 1994, and *Vesicapalpus* Millidge 1991. Hormiga (1999) pointed out that these sulci represent a derived trait, potentially supporting the monophyly of genera exhibiting these sulci.

Males of *Porrhomma cavernicola* retain the triplet, one flagelliform and two aggregate gland spigots necessary for making araneoid sticky silk (Fig. 26; Coddington 1989). The triplet is not found in males of true linyphiines, but is retained in the enigmatic genus *Stemonyphantes* Menge 1866, most erigonines, and in the two mynoglenine genera that have been investigated (Hormiga 2000). It would be useful to investigate the male spinnerets in *Bathyphantes* and other genera known to have lateral sulci.

Males of *P. cavernicola* have epiandrous gland spigots (Fig. 18); the loss of these spigots is considered a synapomorphy of Erigoninae (Miller & Hormiga 2004).

Porrhomma cavernicola lack a tarsal claw on the female pedipalp. Previous phylogenetic analyses concluded that the loss of the tarsal claw was a synapomorphy for Erigoninae (e.g., Hormiga 2000; Miller & Hormiga 2004). The distribution of the tarsal claw on the tree (Fig. 27) makes this conclusion ambiguous. Either the claw was lost independently in the branches leading to erigonines and *Porrhomma*, or the claw was regained in mynoglenines.

An Unusual Stridulatory Organ.—Bishop (1925) described the trochanter II-coxa I stridulatory organ (Fig. 19). Although he attributed the organ to members of the genus *Troglohyphantes*, not *Porrhomma*, Bishop was almost certainly observing *P. cavernicola*. In 1925, *P. cavernicola* (under two names) was placed in *Troglohyphantes*; no other *Porrhomma* species was placed in *Troglohyphantes* at that time (Platnick 2004). Legendre (1963) reviewed sound production in spiders, including the trochanter II-coxa I organ. Citing Bishop (1925), Legendre attributed this organ to *Troglohyphantes* in Europe. However, this organ has not been described for *Troglophyphantes* in its current circumscription (Deeleman-Reinhold 1978, Platnick 2004) or for any other linyphiid genus I am aware of. The organ can be found in at least some epigean *Porrhomma* species (Scharff, pers. comm.). No epigean *Porrhomma* has ever been classified as in *Troglohyphantes*.

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