

CEPHALOTHORACIC SULCI IN LINYPHIINE SPIDERS (ARANEAE, LINYPHIIDAE, LINYPHIINAE)

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ABSTRACT. Pore-bearing cephalothoracic sulci (pits) are described and illustrated for the first time in several linyphiine spiders (Linyphiidae, Linyphiinae). Sulci are reported in members of the genera *Bathypantes* Menge, *Diplostyla* Emerton, *Kaestneria* Wiehle, *Pacifiphantes* Eskov & Marusik, *Porrhomma* Simon, and *Vesicapalpus* Millidge. The phylogenetic implications of the presence of sulci in linyphiines are discussed.

Members of two lineages of linyphiid spiders (Linyphiidae) typically exhibit cephalothoracic sulci, that is, a pair of grooves or pits of varying shape and depth in the cephalic part of the prosoma (see Hormiga 1994, in press, for references). These two lineages are the Mynogleninae and the Erigoninae.

The mynoglenines are a relatively small clade distributed in Africa (Holm 1968), New Zealand (Blest 1979), and Tasmania and some southern Pacific islands (Hormiga, unpubl. data). Mynoglenine sulci are located on the clypeus (Fig. 1–3), below the anterior lateral eyes and are lined with cuticular openings (pores) that connect to glands with secretory cells that exhibit a unique strategy of membrane amplification (Blest & Taylor 1977; Blest & Pomeroy 1978; Blest 1979). The sulci of mynoglenines are present in adults of both sexes and in juveniles (Blest & Taylor 1977); all known mynoglenines have clypeal sulci. These sulci do not seem to play any active role during the courtship (at least in the species studied by Blest & Pomeroy 1978). It has been suggested that the glands that serve these sulci might elaborate defensive secretions because the unique ultrastructure of the clypeal secretory cells is consistent with the synthesis of a toxic product (Blest & Taylor 1977).

The Erigoninae are the largest clade of linyphiids and are distributed throughout the world except New Zealand (Millidge 1988) and Australia (*contra* Wunderlich 1995; see Platnick 1997:419) which lack native species. One of the most conspicuous characteristics of many (but not all) species of erigonines is the presence in males of a vast morphological di-

versity of cephalic modifications, including lobes, turrets, sulci, pits and modified setae. Erigonine sulci usually have a post-ocular position (Figs. 4, 5) and usually have pores associated with glands that are cytologically different from those of the mynoglenine sulci (Blest & Taylor 1977; Schaible et al. 1986; Schaible & Gack 1987). The sulci and other cephalic modifications of erigonines are found only in adult males and play an active mechanical role during courtship: the sulci are gripped by the female cheliceral fangs, as first noted by Bristowe (1931, 1958).

In this paper I report on the discovery of cephalothoracic sulci in several members of the linyphiid subfamily Linyphiinae, including the well-known Holarctic genus *Bathypantes* Menge. This paper brings to light the presence of these structures in linyphiines but does not attempt to cover exhaustively the distribution and morphological variation of sulci across the Linyphiidae.

METHODS

The morphological observations were carried out using a Leica MZAPO dissecting microscope and a Leica DMRM compound microscope. All illustrations were done using a camera lucida and inked on drafting film. Specimens examined with the SEM were first transferred to a vial with 75% ethanol and then cleaned ultrasonically for 1–3 minutes. They were then transferred to absolute ethanol and left overnight. Specimens were air dried and then glued to rounded rivets using an acetone solution of polyvinyl resin. Specimens were coated with a carbon base coat followed by a gold-palladium coat for SEM examina-

tion with the AMRAY 1810 of the Smithsonian Institution's SEM Facility. All the specimens studied (see Table 1) are deposited at the National Museum of Natural History (Smithsonian Institution, Washington, D.C.) unless otherwise stated. In addition to those specimens listed in Table 1, I examined *Haplina diloris* (Urquhart): New Zealand, Fiordland Cascade, in Raoulia, 16 January 1975 (col. & det. A.D. Blest), (Otago Museum, Dunedin) and *Lophomma punctatum* (Blackwall): United Kingdom, Killhope haw., Durham, 2000', 15 June 1966 (J.A.L.C.), (AMNH).

RESULTS

Cephalothoracic sulci were found in all species examined of the linyphiine genera *Bathypantes* (Figs. 6–11), *Diplostyla* Emerton (Figs. 17, 18), *Kaestneria* Wiehle (Figs. 12, 14), *Pacifiphantes* Eskov & Marusik (present only in *P. zakharovi* Eskov & Marusik), *Porrhomma* Simon, and *Vesicapalpus* Millidge (Figs. 15, 16). The sulci were absent in *Linyphantes* Chamberlin & Ivie (five species examined) and in *Pacifiphantes magnificus* (Chamberlin & Ivie) (the males of this latter species remain unknown). The species and specimens studied are given in Table 1. In all these taxa the sulci are located anteriorly in the margin of the carapace, between the chelicerae and the pedipalpal trochanters. The sulcus is a relatively shallow pore-bearing cuticular depression that opens ectoventrally and has an elliptical perimeter (margin). The presence/absence of these pores requires SEM to be discerned. The sulcus is best seen after excision of the pedipalp (e.g., Figs. 6, 9, 15), but in general it can be easily seen without removal of any appendages, particularly from an ectoventral angle. When present, the sulci were found in both males and females of all the 21 species for which both sexes were available for study (see Table 1); no sexual dimorphism in the sulci was discerned with the dissecting microscope.

The morphological details of the sulci of both sexes of *Bathypantes pallidus* (Banks) (Figs. 6–11) and *Kaestneria pullata* (O.P.-C.) (Figs. 12–14) were examined with the SEM. In the female of *Bathypantes pallidus* (Figs. 6–8) the sulci are elliptically shaped (in one specimen the sulcus measured $75 \times 45 \mu\text{m}$). The dorsal and lateral margins of the sulcus

have a slightly sharper edge than the ventral. The sulcus is provided with numerous cuticular pores, particularly in the dorsal half. These pores are not grouped into clusters, as in mynoglennines (Fig. 3), but scattered around, and have a very distinctive wide edge around them (Fig. 8). No cuticular pores can be seen beyond the margin of the sulcus. The sulci of the male of *B. pallidus* (Figs. 9–11) are very similar to those found in females (in one female specimen, Fig. 11, the sulcus measured $78 \times 52 \mu\text{m}$).

The sulci of *Kaestneria pullata* are shallow (Figs. 12–14), particularly in the female, and have a more ventral position under the margin of the carapace. In the females of this species SEM is needed to ascertain the presence of the sulcus which consists of a very shallow depression bearing about 20 cuticular pores (under the dissecting microscope the female sulcus is seen as a slightly darker spot on the cuticle). The male sulcus (Fig. 12) can be seen with the dissecting microscope because the cuticular depression is somewhat deeper than that of the female; in the other aspects these pits are similar to those of the females (Figs. 13–14).

In *Porrhomma convexum* (Westring) the sulci, although shallow, can be clearly seen when viewed under the dissecting microscope. In *Porrhomma borealis* (Banks) (only one female was available for study), *P. montanum* Jackson, *P. microphthalmum* (O.P.-C.) (only males were examined), and *P. pygmaeum* (Blackwall) the sulci are very shallow and oriented ventrally and in both respects are somewhat similar to those of *Kaestneria pullata* (Figs. 12–14).

The sulci of *Pacifiphantes zakharovi* are present in both sexes and are similar, both in position and morphology, to the sulci of *Bathypantes pallidus*.

Males and females of *Lepthyphantes zebra* (Emerton) were examined with the SEM. No cuticular pores were found on the area of the carapace where the sulcus is found in other linyphiines.

DISCUSSION

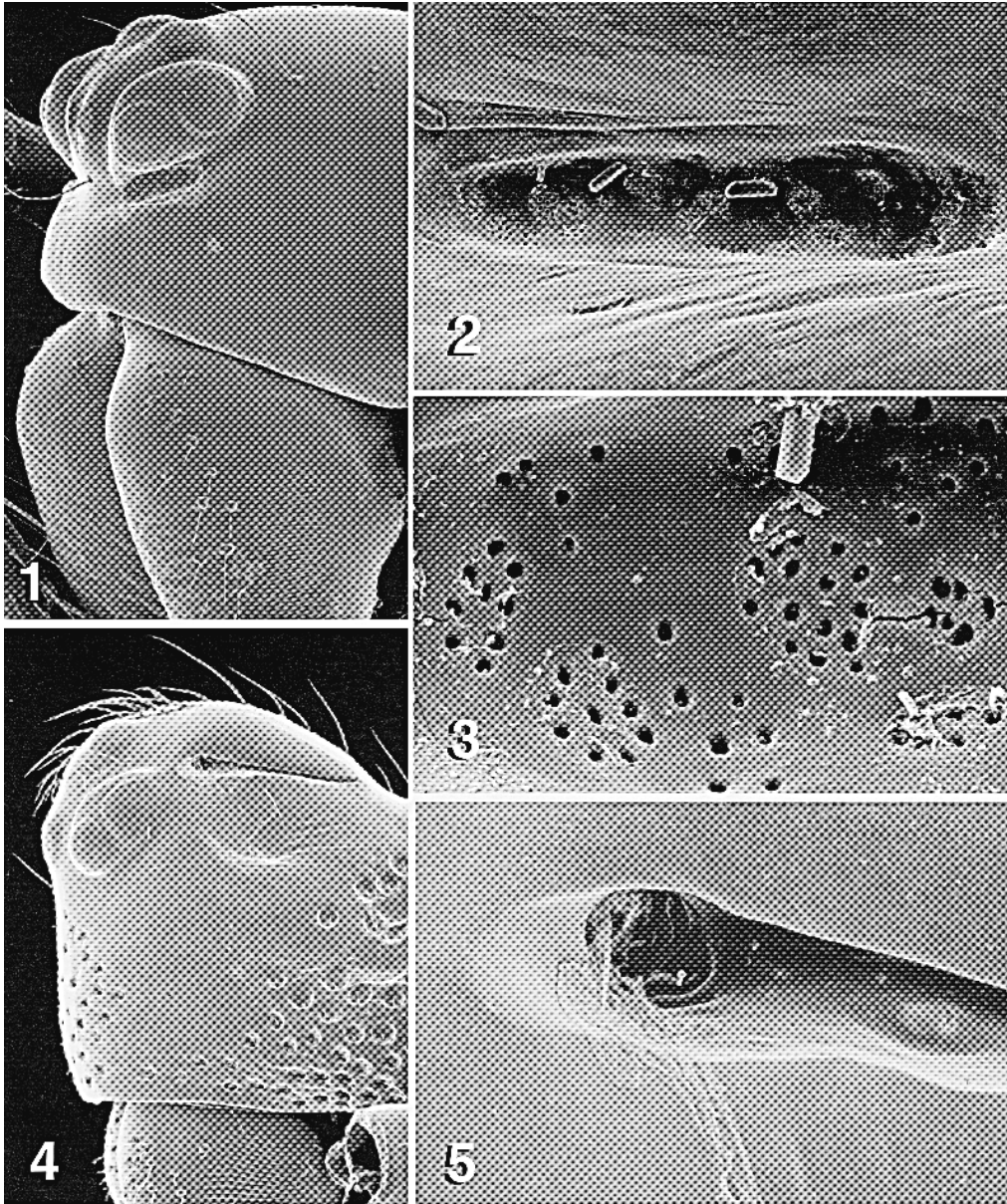
The discovery of cephalothoracic sulci in linyphiines, such as the members of the genus *Bathypantes*, is remarkable because this genus includes some very common spiders (in the Holarctic region) and because these

Table 1.—Taxonomic distribution of cephalothoracic sulci (pits) in the linyphiid taxa studied and specimens examined. “+” indicates sulci present and “-” absent. A “?” indicates that no specimens were available for study; “+?” or “-?” indicates that the observation needs corroboration with scanning electron microscopy (see text for details). Museum abbreviations: AMNH (American Museum of Natural History, New York), CAS (California Academy of Sciences, San Francisco), JZM (J. Zujko-Miller private collection), USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), ZMUC (Zoological Museum, University of Copenhagen, Copenhagen).

Species	Male sulcus	Female sulcus	Country, State or Province	Locality	Collection Date(s)	Museum
<i>Bathyphanes alascensis</i> Banks	+	+	USA, Oregon Washington	Siuslaw Natl. Forest Butler Hill	14 July 1990 10 December 1988	USNM USNM
<i>Bathyphanes approximatus</i> (O. P.-C.)	+	+	Denmark	Bremerholmsaret	13 July 1920	ZMUC
<i>Bathyphanes alboventris</i> (Banks)	?	+	USA, Tennessee	Rainbow Cave	8 August 1981	USNM
<i>Bathyphanes bishopi</i> (Ivie)	+	+	USA, North Carolina	Great Smoky Mts. N.P.	7 August 1961	USNM
<i>Bathyphanes brevipes</i> (Emerton)	+	+	USA, Washington	Thurston Co., Evergreen State College	16 December 1993	JZM
<i>Bathyphanes eumenis</i> (L. Koch)	+	+	Russia, NE Siberia	Kamchatka	17 September 1996	USNM
<i>Bathyphanes gracilis</i> (Menge)	+	+	Russia, NE Siberia	Kamchatka	18 September 1996	USNM
<i>Bathyphanes keeni</i> (Emerton)	+	+	USA, California	Mendocino woodlands	20 August 1990	USNM
<i>Bathyphanes nigrinus</i> (Westring)	+	+	Canada, Brit. Col. Denmark	Vancouver	4-9 July 1988	USNM
<i>Bathyphanes orica</i> Ivie	?	+	USA, Washington	Copenhagen Thurston Co., Evergreen State College	September 1989 25 October 1992	ZMUC JZM
<i>Bathyphanes pallidus</i> (Banks)	+	+	USA, Maryland	Patuxent Wildlife Refuge Center	2 June 1994	USNM
<i>Bathyphanes pogonias</i> Kulezynski	+	+	Russia, Kurile Isles	Bering Isld	July-August 1987	USNM
<i>Bathyphanes reprobus</i> (Kulezynski)	?	+	Russia, NE Siberia	Lankovaya River	12-19 August 1992	USNM
<i>Bathyphanes setiger</i> (F. O. P.-C.)	+	?	Denmark	Losø, Blødens vestide	20 July 1946	ZMUC
<i>Bathyphanes simillinus</i> (L. Koch)	?	+	Denmark	Greenland, Disko	9 July 1962	ZMUC
<i>Bathyphanes waneta</i> Ivie	+	+	USA, Washington	Brooks Mem. State Pk.	1 March 1980	USNM
<i>Bathyphanes weyeri</i> (Emerton)	+	+	USA, West Virginia	W. Va. Univ. Forest	26 June-9 July 1989	USNM
<i>Bathyphanes</i> sp. Oregon	?	+	USA, Oregon	Shore Acres State Pk.	16 August 1990	USNM
<i>Diplostyla concolor</i> (Wider)	+	+	USA, Massachusetts	Quisset	10 June 1988	USNM
<i>Kaesteria dorsalis</i> (Wider)	-?	-?	Sweden	Sjugarn, Gotland	14 July 1936	ZMUC
<i>Kaesteria pullata</i> (O.P.-C.)	+	+	Russia, NE Siberia	Lankovaya River	12-19 August 1992	USNM
<i>Pacifiphantes magnificus</i> (Ch. & Ivie)	?	-	USA, Washington	5 mi. E of McCleary	26 August 1952	AMNH

Table 1.—Continued

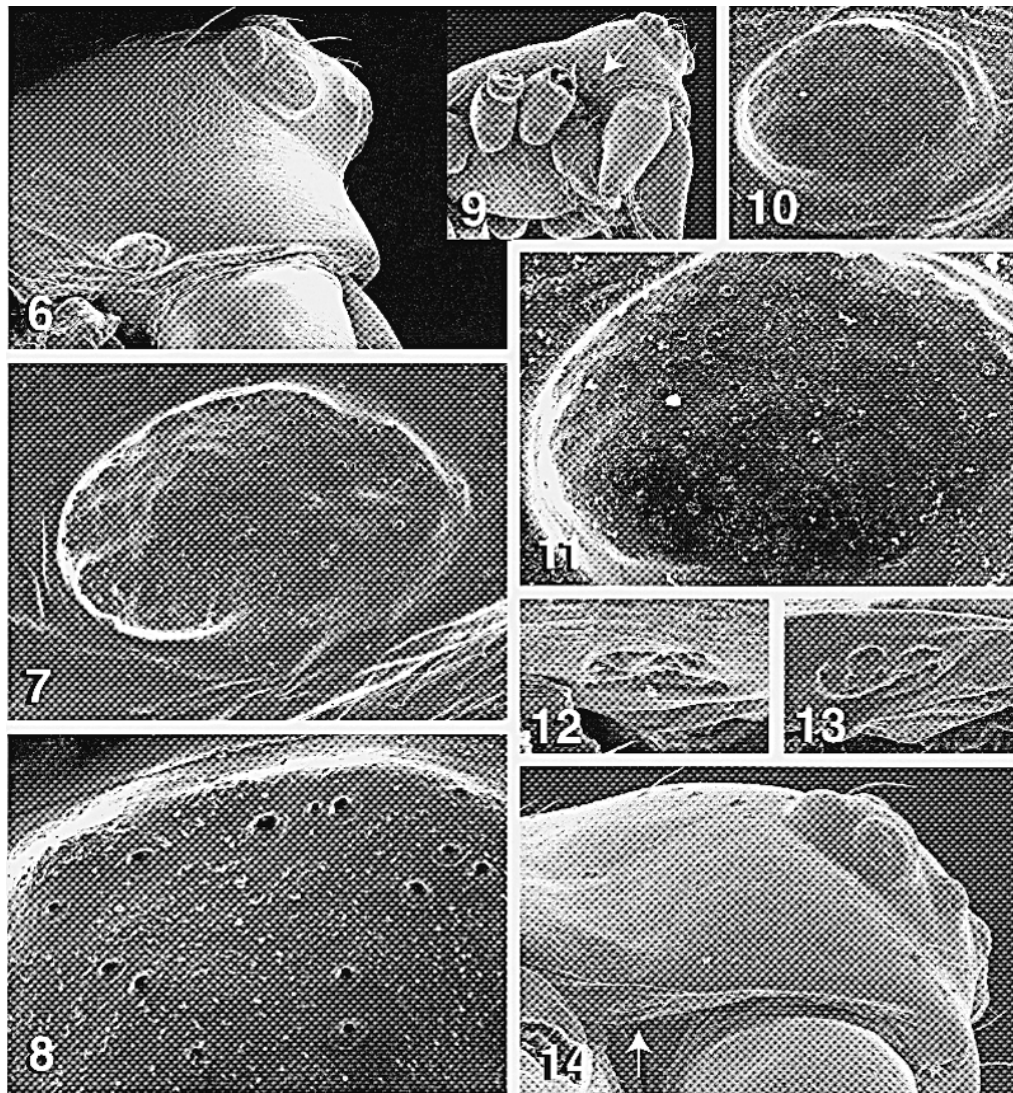
Species	Male sulcus	Female sulcus	Country, State or Province	Locality	Collection Date(s)	Museum
<i>Pacifiphantes zakharovi</i> Eskov & Marusik	+	+	Russia	Vladivostok	30 September 1997	USNM
<i>Porrhomma borealis</i> (Banks)	?	+?	Russia, NE Siberia	Magadan Area, Ola Riv. Upper flow	15–18 September 1992	USNM
<i>Porrhomma convexum</i> (Westring)	+	+	Iceland	Molifellsa, Skagafj	13 July 1933	ZMUC
<i>Porrhomma montanum</i> Jackson	+	+	Denmark	Hestheaven, Rønde	July–September 1994	ZMUC
<i>Porrhomma microphthalmum</i> (O.P.-C.)	+	?	Denmark	Hestheaven, Rønde	July–September 1994	ZMUC
<i>Porrhomma pygmaeum</i> (Blackwall)	+	+	Denmark	Zealand, Tisvildeleje	19–20 May 1991	ZMUC
<i>Vesicapalpus simplex</i> Millidge	+	+	Brazil	Parque Nacional da Serra dos Orgãos	11 November 1959	AMNH
<i>Vesicapalpus</i> sp. Colombia	+	+	Colombia, Huila	P.N.N. Puracé, Laguna de San Rafael	15 February 1998	USNM
<i>Lepthyphantes zebra</i> (Emerton)	–	–	USA, Georgia	Ellicott Rock Wilderness Area	24 May 1993	USNM
<i>Linyphantes aeronauticus</i> (Petrunkevitch)	–	–	USA, Washington	Douglas Co., Hw2, mi. 135 rest stop at Lake Entiat	20 March 1980	USNM
<i>Linyphantes anacortes</i> Chamberlin & Ivie	–	–	USA, Oregon	Curry Co., Brookings	19 June 1952	USNM
<i>Linyphantes orcinus</i> (Emerton)	–	–	USA, Washington	Clallam Co., Salt Creek mouth	23 May 1987	USNM
<i>Linyphantes pualla</i> Chamberlin & Ivie	–	–	USA, Washington	Mason Co., Brown Creek Horse Camp	15 October 1993	JZM
<i>Linyphantes victoria</i> Chamberlin & Ivie	–	–	USA, Washington	Thurston Co., Evergreen State College	25–27 October 1992	JZM



Figures 1–5.—Cephalothoracic sulci in Linyphiidae. 1. *Haplinis diloris* (Urquhart) (Mynogleninae), female, lateral; 2, 3. Detail of *Haplinis diloris* male lateral subocular sulcus (right); 4. *Lophomma punctatum* (Blackwall) (Erigoninae), male, lateral; 5. Detail of *Lophomma punctatum* male postocular sulcus (left).

pits are easily observable with the dissecting microscope. Consequently I was very reluctant to believe that these distinct structures remained undescribed. The only taxonomic revision of *Bathyphantes* is that of Ivie (1969) for Nearctic species. In his monograph Ivie described and illustrated 27 spe-

cies of *Bathyphantes* (some of them are currently classified in other genera), but he made no reference to the sulci. None of the many isolated taxonomic descriptions of *Bathyphantes*, *Diplostyla*, *Porrhomma*, and *Vesicapalpus* species I have checked mention these pits. It is difficult to explain how such



Figures 6–14.—Cephalothoracic sulci in Linyphiidae. 6. *Bathyphantes pallidus* (Banks), female, lateral; 7. *Bathyphantes pallidus*, female sulcus (right); 8. Detail of *Bathyphantes pallidus* female sulcus (right); 9. *Bathyphantes pallidus*, male, ventrolateral (arrow points to sulcus); 10. *Bathyphantes pallidus*, male sulcus (right); 11. Detail of *Bathyphantes pallidus* male sulcus (right); 12. *Kaestneria pullata* (O.P.-C.), male cuticular pores (right); 13. *Kaestneria pullata*, female cuticular pores (right); 14. *Kaestneria pullata*, female, ventrolateral (arrow points to location of cuticular pores).

a conspicuous structure has remained undocumented for so long.

The presence of cephalothoracic pore-bearing cuticular depressions in linyphiines is of relevance for the study of the evolution of cephalic specializations. Unfortunately, detailed understanding of the evolutionary history of these structures is severely hindered by the lack of explicit hypotheses on the phyloge-

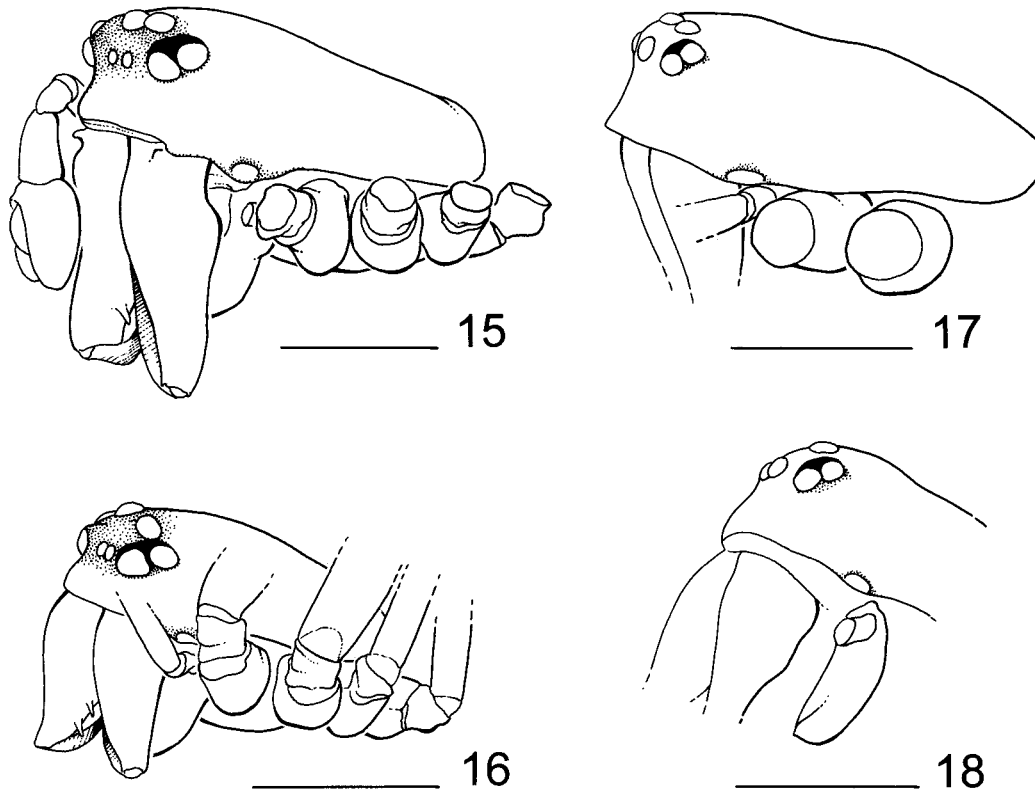
netic structure of the Linyphiidae. In my opinion, one of the main questions concerning the evolution of linyphiid sulci is whether myoglenine and erigonine sulci are homologous structures, as argued by Blest (1979), Blest & Taylor (1977), Blest & Pomeroy (1978) and Millidge (1993). In an initial assessment of this problem (Hormiga 1994) I concluded that although the non-homology hypothesis was

more parsimonious, the question could not be rigorously tested “until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands)” were studied. Recent progress in the phylogenetics of erigonines (Hormiga in press) supports the non-homology hypothesis of the erigonine and mynoglennine sulci. This is a result of the basal cladistic placement (within the Erigoninae) of a number of lineages in which neither the cuticular pores nor the sulci are present. Given such a cladogram topology parsimony requires independent origins (i.e., non-homology) of the sulci in erigonines and mynoglennines; this occurs even when the cuticular pores of erigonines and mynoglennines are coded as homologous in the cladistic analysis. The discovery of sulci in linyphiines suggests that this “character” is even more homoplasious than initially argued because several independent origins of sulci in the Linyphiidae are required: one in mynoglennines, at least two in erigonines, and one or more instances in linyphiines (unless mynoglennine and linyphiine sulci are homologous). All described mynoglennines have subocular sulci (Blest 1979), and the presence of such sulci (and their associated glands) is synapomorphic for this subfamily (Hormiga 1994, in press). The phylogenetic patterns of sulci and cuticular pores in erigonines are much more complex (Hormiga in press) and our knowledge is still very preliminary. Despite this, it seems that based on the taxonomic distribution of these characters and on my cladistic reconstructions, there are multiple origins of the prosomic cuticular pores and at least two independent origins for sulci in erigonines (pores are more widely distributed across taxa than sulci).

In linyphiines prosomic cuticular pores had been described in *Bolyphantes* (Blest & Taylor 1977). In *B. luteolus* (Blackwall) pores are found both in the male and the female (*contra* Blest & Taylor 1977: 91) (Hormiga in press). So far no cephalothoracic sulci have been documented in linyphiines (other than those described in this paper). Because there is no explicit cladistic hypothesis for the genera (or an adequate subset of genera) of Linyphiinae, at the present time it is not possible to provide a robust hypothesis about the origin of the sulci within this subfamily. Nevertheless the genera *Bathyphantes*, *Diplostyla* and *Kaestneria* have been traditionally considered close rela-

tives (this has been largely based on overall similarity; e.g., Wiehle (1956) or Millidge (1984)), and several species of these genera have changed generic placement within this cluster of genera. The presence of cephalothoracic sulci in *Bathyphantes*, *Diplostyla*, *Kaestneria*, and *Porrhomma* is a derived trait and thus a potential putative synapomorphy supporting the monophyly of these genera. The genitalic morphology of these four genera seems to be consistent with this hypothesis (e.g., Millidge 1977), but this requires further study and testing. Chamberlin & Ivie (1942: 45) and Ivie (1969: 2) suggested that *Bathyphantes* and *Linyphantes* were closely related because they agree in “in most general characters.” The five species of *Linyphantes* that I have examined, including the type species *L. aeronauticus* (Petrunkevitch), lack sulci and their palp morphology shares little in common with the palp morphology of *Bathyphantes*. To this date no synapomorphies have yet been proposed that could potentially support the monophyly of *Linyphantes* plus *Bathyphantes*. *Pacifiphantes magnificus*, recently transferred from *Bathyphantes* by Eskov & Marusik (1994) using phenetic criteria, also lacks sulci (although males remain unknown) although the pits are present in the both sexes of the type species, *Pacifiphantes zakharovi*. The phylogenetic placement of *Vesicapalpus* remains even more obscure. This monotypic Neotropical genus is known in the literature after a single male specimen (the holotype of *Vesicapalpus simplex* Millidge). Millidge (1991) did not document the presence of sulci in his sparse description of *V. simplex*. Sulci are present in both sexes of *Vesicapalpus simplex* (Figs. 15, 16) and in an undescribed species from Colombia (Hormiga unpubl. data). Whether the sulci of *Vesicapalpus* are or not homologous to the sulci of other linyphiines cannot be answered in absence of a phylogenetic hypothesis for the relationships of these taxa.

Outside Linyphiidae, but within Araneoidea, similar pore-bearing sulci are found in most members of the family Anapidae (Platnick & Forster 1986, 1989, 1990). Platnick & Forster (1989: 135) suggest that the presence in both sexes of glandular openings at the anterolateral corners of the carapace may be a synapomorphy of Anapidae. The cuticular openings of anapids are located in a pit on the



Figures 15–18.—Cephalothoracic sulci in Linyphiidae. 15. *Vesicapalpus simplex* (Millidge), male (holotype) from Argentina (right side reversed); 16. *Vesicapalpus simplex* female from Brazil; 17. *Diplostyla concolor* (Wider), male from Massachusetts; 18. *Diplostyla concolor*, female from Massachusetts. (Scale bars = 0.5 mm)

edge of the carapace, just above the endites (see figs. 1–4 in Platnick & Forster 1986). In *Minanapis* Platnick & Forster there is no pit and the pores open directly on the surface of the carapace. In other anapids, such as *Gertschanapis* Platnick & Forster and *Maxanapis* Platnick & Forster, the cephalic pit has shifted onto a separate sclerite that is reflexed under the lateral margin of the carapace (Platnick & Forster 1989, 1990) in an analogous situation to the condition found in *Kaestneria pullata* (cf. figs. 271 and 272 in Platnick & Forster 1989).

In sum, the pore-bearing sulci of linyphiines provide another instance of homoplasy in the evolution of cephalic specializations in linyphiids. Preliminary data presented here suggests that the study of this character will be important for phylogenetic reconstruction. Progress in understanding the evolutionary chronicle of these complex character systems

will have to wait for more data on their biological role and function (at present, the function of the sulci in mynoglennines and linyphiines remains unknown), for more information on its taxonomic distribution, and for a more detailed understanding of the higher level phylogenetics of this large group of araneoid spiders.

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