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Comb-hairs on the fourth tarsi in pholcid spiders (Araneae, Pholcidae)

Bernhard A. Huber and **Nadine Fleckenstein**: Alexander Koenig Research Museum of Zoology, Adenauerallee 160, 53113 Bonn, Germany. E-mail: b.huber.zfmk@uni-bonn.de

Abstract. Comb-hairs on the fourth tarsi of males and females are a classical theridioid character, but they also occur in pholcids. Previous studies on *Pholcus phalangioides* (Fuesslin 1775) have shown that in this species the comb-hairs function in the context of sticky silk wrap attack just as in theridiids. Here we investigate pholcid comb-hairs in a comparative way, studying the tarsal hairs of representatives of 42 pholcid genera with the SEM. We found two principal morphologies, a simple and a complex type of comb-hair. We found two principal types of comb-hair distribution on the tarsus: in distal patches or in ventral rows, but intermediate types also occur. Character mapping suggests that simple comb-hairs are derived from complex ones, and that distal patches are plesiomorphic, ventral rows derived. We speculate that pholcid comb-hairs may be derived from hairs (the "accessory claws") that grasp silk in functional correlation with the median claw. In a female shock-frozen during wrap attack, the silk line passed through the notch of a comb-hair, but several functional details (silk grasping and releasing, function of different hair branches) remain unanswered.

Keywords: Sticky silk wrap attack, silk manipulation, morphology

Comb-hairs on the fourth tarsi are a classic character of theridioids (Theridiidae and Nesticidae). In these spiders, comb-hairs are thought to function in the context of sticky silk wrap attack ("ss-wrap"). In contrast to other spiders, theridiids and nesticids wrap prey with sticky silk rather than with dry silk (e.g., Nielsen 1932; Kirchner & Kullmann 1972; Carico 1978; Coddington 1986; Whitehouse 1987; Forster et al. 1990; Griswold et al. 1998). The fact that this is done with the fourth tarsi strongly suggests this functional interpretation of comb-hairs even though the exact mechanics of the interactions between comb-hair and silk remain unknown.

Other than theridioids, only the distantly related Pholcidae are known to use sticky silk during wrap attack, at least during the early phases of wrapping (Eberhard 1992; Japyassú & Macagnan 2004). The convergence goes even further in that pholcids, too, use their fourth legs to wrap prey (e.g., Jackson & Brassington 1987; Kirchner & Opderbeck 1990; Japyassú & Macagnan 2004), and recent studies have shown that several genera within the family have comb-hairs on the fourth tarsi that show considerable similarity to those of certain theridiid taxa (*Belisana*: Huber 2005a; *Spermophora*: Huber 2005b; *Carapoia*: Huber 2005c; *Metagonia*: Huber et al. 2005; *Leptopholcus*: Huber & Wunderlich 2006).

This striking convergence strengthens the idea that the comb-hairs are directly correlated with the manipulation of sticky silk. However, just as in theridiids, the details of interaction remain unknown. Previously, only the study by Kirchner & Opderbeck (1990) has looked in some detail at the comb-hairs in *Pholcus phalangioides* (Fuesslin 1775). These authors photographed the spider during wrapping, showing that the fourth tarsus indeed holds the silk line, and it is quite evident from their figure 5 that it is not the tarsus tip (the claws) that grasp the line but the more proximal section.

The present study is the first to give a wide comparative overview of pholcid comb-hairs that were discovered long ago (Lebert 1874) in *P. phalangioides* but that were until recently never searched for in other pholcids. A few recent studies (above) have shown variation within the family, both in hair structure and position, but the data were too scarce to allow a meaningful evolutionary interpretation. By mapping details of comb-hair morphology on cladograms derived from other morphological and from molecular data we trace the evolution of comb-hairs in Pholcidae.

METHODS

We studied the fourth tarsal hairs of representatives of 42 pholcid genera and of three outgroups (Table 1) using SEM (Hitachi S-2460). In addition, in some species we scanned all tarsi of both males and females. In *P. phalangioides* we also studied young juveniles (~2.5 mm total body length). For character mapping we used a composite cladogram derived from recent morphological and molecular work on pholcid phylogeny (Huber 2000, 2001, 2003a, b, c, 2005a, b; Bruvo-Mađarić et al. 2005; Huber & El Hennawy 2007; Astrin et al. 2007; B.A. Huber unpublished data on *Pholcus* and close relatives). In order to see the details of hair-silk interaction, we freeze-fixed four *P. phalangioides* and two *Psilochorus simoni* (Berland 1911) specimens during wrap attack using a freezing spray (Reparil® Ice-Spray Madaus). Specimens were immediately transferred to 80% ethanol at −20° C and kept at this temperature for one week. The fourth legs were then detached from the spider and studied with the SEM. Vouchers of all species studied and SEM stubs are deposited at the Alexander Koenig Research Museum of Zoology, Bonn.

RESULTS

Except for the two Old World ninetines we studied (*Ninetis*, *Nita*), we found comb-hairs in all pholcid species. In those species where all tarsi were examined, comb-hairs occurred only on the fourth tarsi. We found no evidence for sexual dimorphism. Comb-hairs were also present in *P. phalangioides* juveniles. There was considerable variation both in comb-hair morphology and distribution on the fourth tarsi.

Comb-hair morphology.—We found two main types of comb-hairs, each one widely distributed among genera, and a few deviant types restricted to single species. We call the two main types the "*Pholcus*-type" and the "*Belisana*-type." The

Table 1.—Taxa studied, sexes studied, and previous publications showing pholcid tarsal comb-hairs. Asterisks indicate species for which all tarsi were examined.

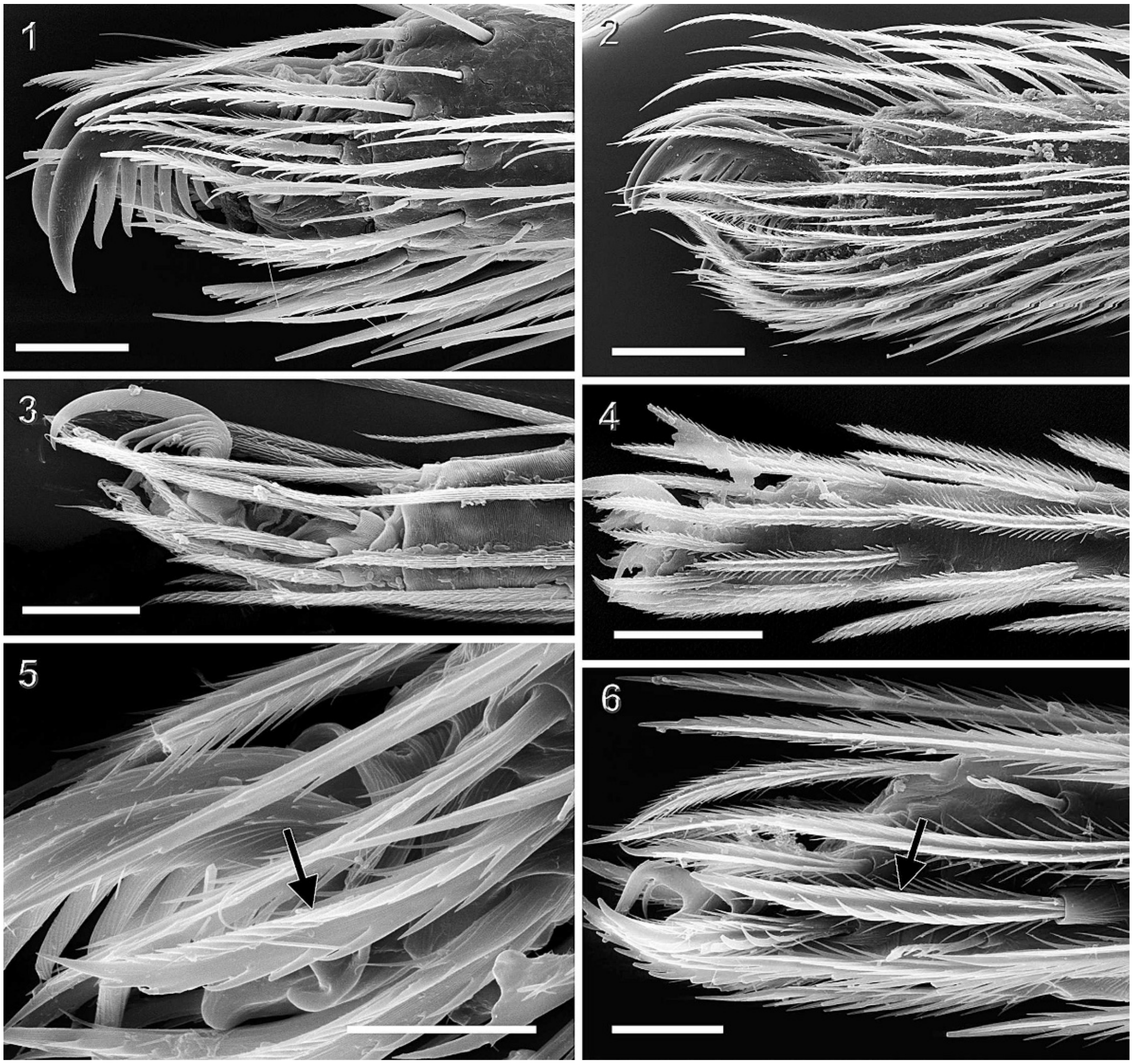
Species	m/f	Previous publications
Outgroups		
Diguetia signata Gertsch 1958	f	
Ochyrocera sp. (Costa Rica, Escazú)	m	
Plectreurys tristis Simon 1893	f	
Ninetinae		
Aucana kaala Huber 2000	m	
Ibotyporanga naideae Mello-Leitão 1944	f	
* *Ninetis toliara* Huber & El Hennawy 2007	m	
* *Nita elsaff* Huber & El Hennawy 2007	m	
Pholcophora americana Banks 1896	m/f	
New World Clade		
Anopsicus chickeringi Gertsch 1982	m	
Carapoia spp.	f	Huber 2005c
Chibchea ika Huber 2000	m	
Ciboneya antraia Huber & Pérez 2001	m	
Mecolaesthus longissimus Simon 1893	m	
Mesabolivar eberhardi Huber 2000	m	
Mesabolivar sp. (“Brazil 7”)	m	
Mesabolivar yuruani (Huber 2000)	f	
* *Modisimus guatuso* Huber 1998	m/f	
Priscula sp. (“Venezuela 1”)	m	
Tainonia sp. (“samana”)	m/f	
Holocnemines I		
Artema atlanta Walckenaer 1837	f	
Holocneminus piritarsis Berland 1942	f	
Physocyclus globosus (Taczanowski 1874)	f	
Trichocyclus nullarbor Huber 2001	f	
Holocnemines II		
Crossopriza lyoni (Blackwall 1867)	f	
Holocnemus pluchei (Scopoli 1763)	m	
Hoplopholcus minotaurus Senglet 1971	f	
* *Smeringopina pulchra* (Millot 1941)	f	
Smeringopina sp. (“USNM 9”)	f	
Smeringopus natalensis Lawrence 1947	m	
Pholcinae – ‘Basal’ Taxa		
* *Belisana* spp.	m/f	Huber 2005a
Buitinga asax Huber 2003	m	
Khorata khammouan Huber 2005	m/f	
Metagonia conica (Simon 1893)	m	
Metagonia reventazona Huber 1997	m	
Metagonia spp.	m/f	Huber et al. 2005
Nyikoa limbe Huber 2007	m/f	
Paramicromerys scharffi Huber 2003	f	
Quamtana bonamanzi Huber 2003	f	
Spermophora senoculata (Dugès 1836)	f	
Spermophora usambara Huber 2003	m	
Spermophora spp.	f	Huber 2005b
Spermophorides cuneata (Wunderlich 1987)	m	
Spermophorides elevata (Simon 1873)	m	
Zatavua vohiparara Huber 2003	f	
Pholcinae – *Pholcus* and Close Relatives		
Calapnita phyllicola Deeleman-Reinhold 1986	m	
Leptopholcus spp. (Dom. Rep.)	m/f	Huber & Wunderlich 2006
Leptopholcus hispaniola Huber 2000	m/f	
Micromerys daviesae Deeleman-Reinhold 1986	m	
Micropholcus fauroti (Simon 1887)	m	
Ossinissa justoi (Wunderlich 1992)	f	
Panjange mirabilis Deeleman-Reinhold 1986	f	
Pehrforsskalia conopyga Deeleman-Reinhold & van Harten 2001	m	
* *Pholcus opilionoides* (Schrank 1781)	m/f	
Pholcus phalangioides (Fuesslin 1775)		Kirchner & Opderbeck 1990
Uthina luzonica Simon 1893	f	

Pholcus-type of comb-hair is simple; it consists basically of a main shaft that is distally slightly curved or hooked and about four to six hooked branches directed to the same side (Figs. 25–31). The *Belisana*-type of comb-hair is considerably more complex. It consists of a main shaft with three distinctive rows of branches (Figs. 5–24): a ventral (with respect to the tarsus) row of about 6–12 curved (or slightly hooked) branches, a dorsal row of about 6–10 fairly straight and usually thin branches, and between these rows another row of about 10–30 short straight branches. Deviant types of hairs occur in *Artema atlanta* Walckenaer 1837 (*Belisana*-type but unusually strong branches in the median row, Figs. 17, 18), *Priscula* sp. (only two rows of branches visible in lateral view, Fig. 11), and some *Spermophora* and Pacific *Belisana* species (e.g., *B. airai* Huber 2005, *B. fiji* Huber 2005; high number of ventral branches very close together, Fig. 24; see also figs. 477, 639 in Huber 2005a).

Comb-hair length ranges from about 40 to 160 µm for both types and seems to be closely related to the overall size of the spider. In *P. phalangioides* spiderlings, comb-hair length was about 45–50 µm, in adults 90–105 µm. Interestingly, the short comb-hairs in juveniles tended to have more rather than fewer branches (4–5 versus 3–4 in adults).

Comb-hair distribution.—Pholcid comb-hairs show two main types of distribution on the tarsus. They are either limited to patches of hairs distally on the tarsus (Figs. 5–12) or they are aligned ventrally (or slightly prolaterally) in a single row (Figs. 19–30). In the first case, patches of hairs occur both on the prolateral and retrolateral sides, but the prolateral patch is more developed, both in terms of number of hairs (usually about 3–6) and in the distinctiveness of the comb-hairs themselves. The retrolateral patch may consist of no more than one or two modified hairs. Additional (apparently intermediate) types of distribution were found in certain “holocnemines” where the prolateral patches of hairs extend farther towards the basis of the tarsus, in some cases resulting in two ventral-prolateral rows (Fig. 14) of hairs spread over almost the entire length of the tarsus.

Character mapping and optimization.—Character mapping on the cladogram in Fig. 32 allows the reconstruction of the evolutionary simplification of comb-hair morphology within Pholcidae. The *Pholcus*-type of comb-hair evolved once within Pholcinae, supporting a group of genera closely related to *Pholcus*. The origin of the plesiomorphic *Belisana*-type of hair



Figures 1–6.—Hairs on tarsus 4 tip, outgroups and ninetines. 1. *Diguetia signata*, female right tarsus 4, prolateral; 2. *Plectreurys tristis*, female right tarsus 4, prolateral; 3. *Ochyrocera* sp., male left tarsus 4, retrolateral; 4, *Nita elsaff*, male left tarsus 4, retrolateral; 5. *Ibotyporanga naideae*, female right tarsus 4, prolateral; 6. *Pholcophora americana*, female right tarsus 4, prolateral (main claws missing). Arrows point to comb-hairs. Scale lines: 20 µm (3, 5, 6), 40 µm (4), 60 µm (1), 200 µm (2).

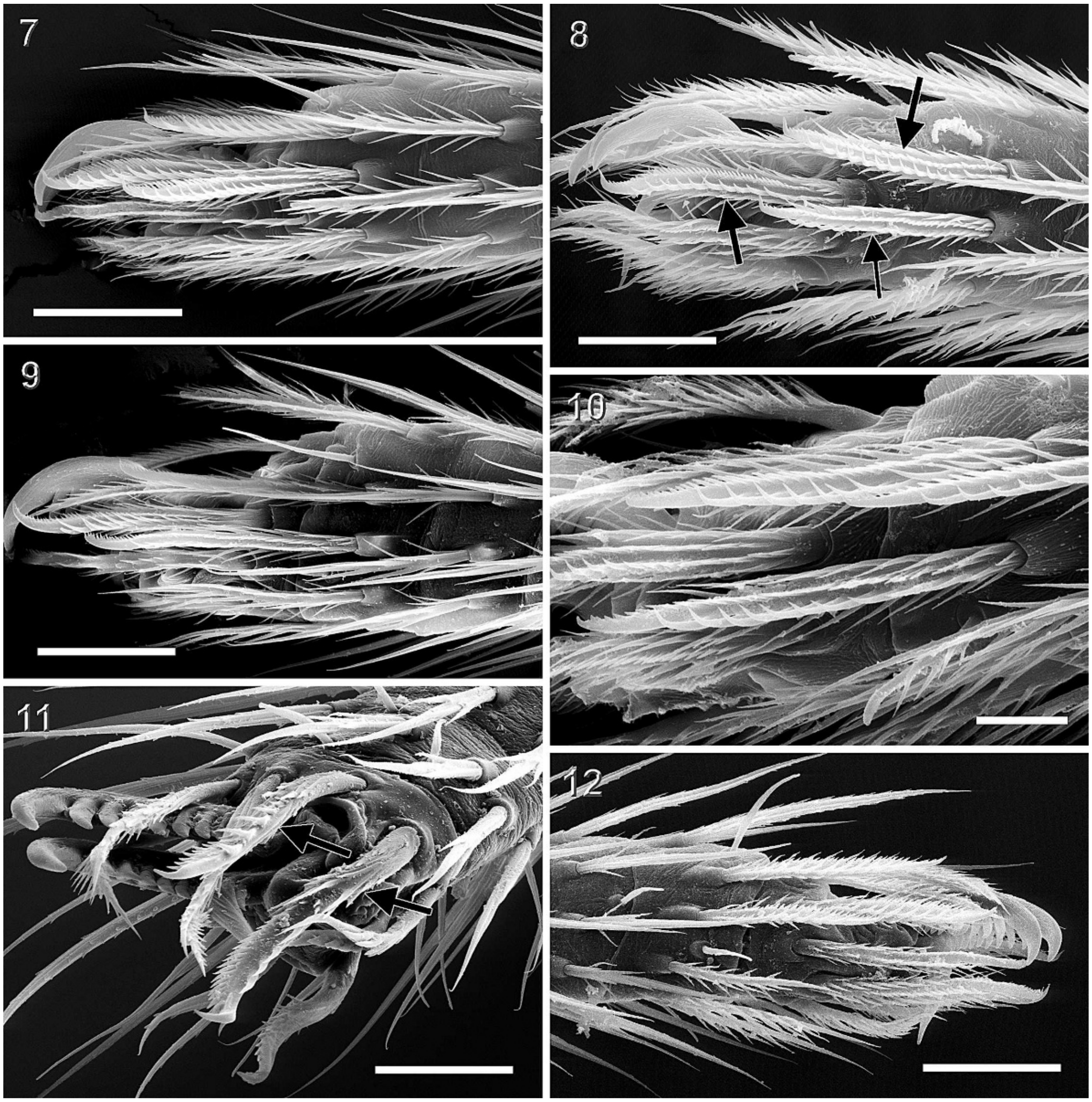
is at or near the base of Pholcidae, but the optimization is ambiguous. The cladogram suggests either one origin at the base of Pholcidae and subsequent loss in a subgroup of ninetines (this is the scenario shown in Fig. 32), or at least two independent gains.

With respect to comb-hair distribution on the tarsus, optimization suggests that a distal patch is plesiomorphic, ventral rows (double or single) are derived. The origin of ventral rows may have occurred more than once, at the base of Pholcinae and in certain "holocnemines." Another possible interpretation (which is shown in Fig. 32) is that comb-hairs arranged in rows are a synapomorphy of a subgroup of "holocnemines" + pholcines (see also Discussion below).

Comb-hair function.—Of the six specimens that were freeze-fixed during prey-wrapping, only one had a silk line in contact with a comb-hair. The silk line passed through the notch formed by one of the hooked branches (Fig. 31). In the other five specimens, no interaction between silk and comb-hairs could be observed; they had either been frozen at the wrong moment or the manipulations at preparing the object for the SEM had destroyed the functional contact between silk and comb-hairs.

DISCUSSION

Comb-hair evolution.—The data above suggest that pholcid comb-hairs evolved either once or twice. This uncertainty is related to the question of ninetine monophyly. If ninetines are in fact monophyletic (as in Fig. 32), then comb-hairs appear to have evolved either at least twice or once with at least one reversal. Paraphyletic ninetines, for example with Old World ninetines as sister to all other pholcids including New World ninetines, would suggest a single origin of pholcid comb-hairs without reversal. However, morphological data suggest that the Old World genus *Nita* is more closely related to some New World ninetines than to *Ninetis* (Huber & El Hennawy 2007). Ninetine monophyly is based mostly on morphological



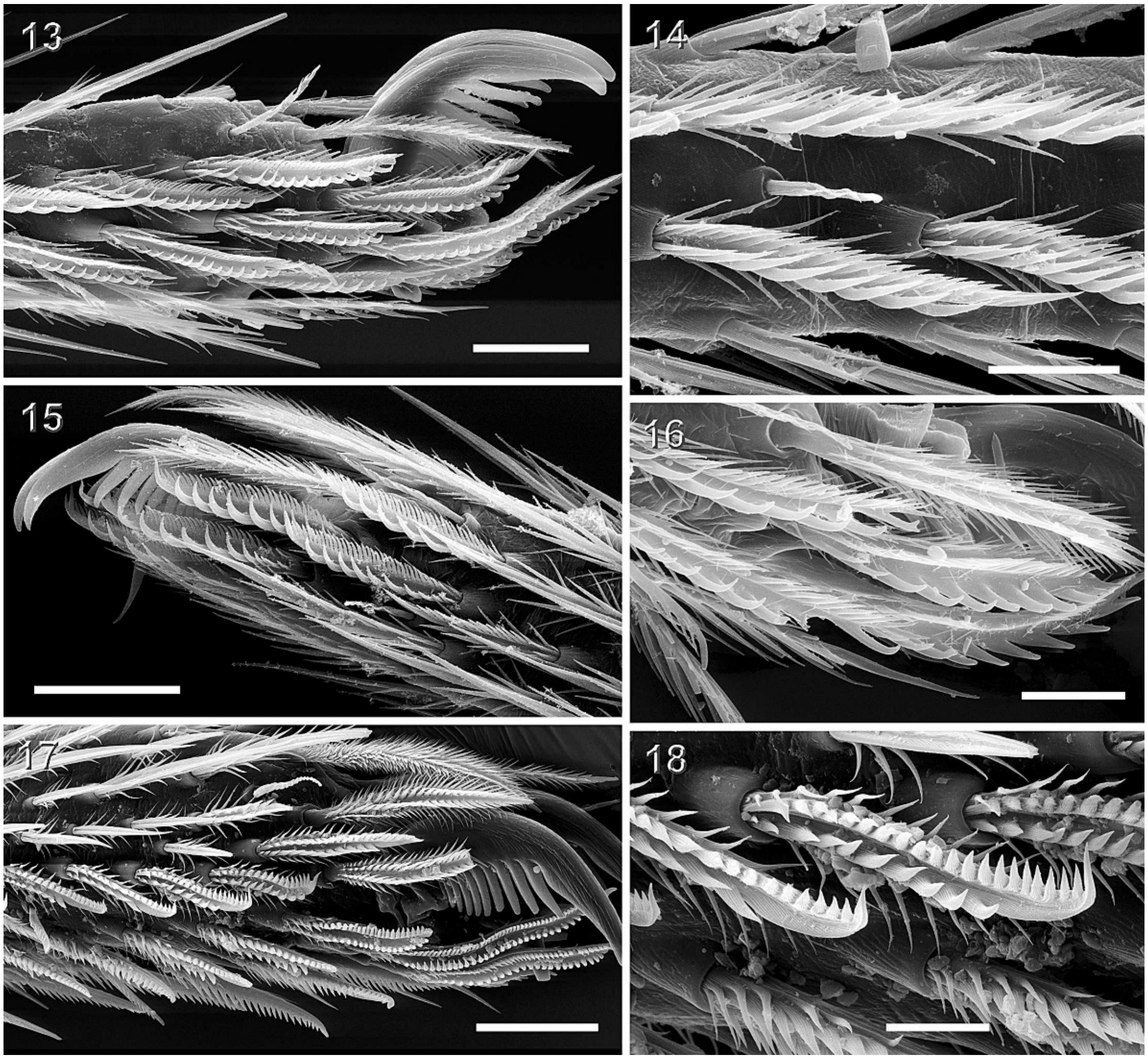
Figures 7–12.—Hairs on tarsus 4 tip, New World clade. 7. *Modisimus guatuso*, female right tarsus 4, prolateral; 8. *Carapoia una* Huber 2005, female right tarsus 4, prolateral; 9. *Mesabolivar eberhardi*, male right tarsus 4, prolateral; 10. *Mesabolivar yuruani*, female right tarsus 4, prolateral-ventral; 11. *Priscula* sp., male right tarsus 4, prolateral-distal; 12. *Tainonia* sp., female left tarsus 4, prolateral. Arrows point to selected comb-hairs. Scale lines: 10 µm (10), 30 µm (8), 40 µm (7), 50 µm (9), 60 µm (11, 12).

characters, some of which may not be independent due to their correlation with small size (Huber 2003d; Huber & Brescovit 2003). Molecular data appear promising for a solution of this question, but ninetines are notoriously rare in collections and only a few species have been included in recent molecular phylogenetic analyses (Bruvo-Mađarić et al. 2005; Astrin et al. 2007).

Our data provide clear evidence for morphological simplification in pholcid comb-hair evolution. The simple *Pholcus*-type of comb-hair characterizes a highly derived clade within pholcines and the data unambiguously support its derivation from the complex *Belisana*-type. This clade of presently nine genera (all included in Table 1) is currently under revision by the first author, and preliminary cladistic analysis suggests that it is supported by at least one further morphological character, a bulbal apophysis traditionally called an appendix. The lower number on branches in adult than in juvenile *P. phalangioides* comb-hairs could be interpreted as ontogenetic evidence for the evolutionary simplification of comb-hair morphology.

Comb-hair distribution provides further (though weak) evidence against holocnemine monophyly. One subgroup of holocnemines (*Holocnemus*, *Crossopriza*, *Smeringopus*, *Hoplopholcus*, *Smeringopina*) shares with pholcines the derived condition of comb-hairs not restricted to distal patches but being spread over most of the tarsus length. Holocnemine monophyly has been questioned before, first because morphological data appeared unconvincing (Huber 2000), later because molecular data suggested polyphyly (Bruvo-Mađarić et al. 2005; Astrin et al. 2007).

The fact that pholcid comb-hairs originated distally on the tarsus suggests that they may be derived from those hairs that

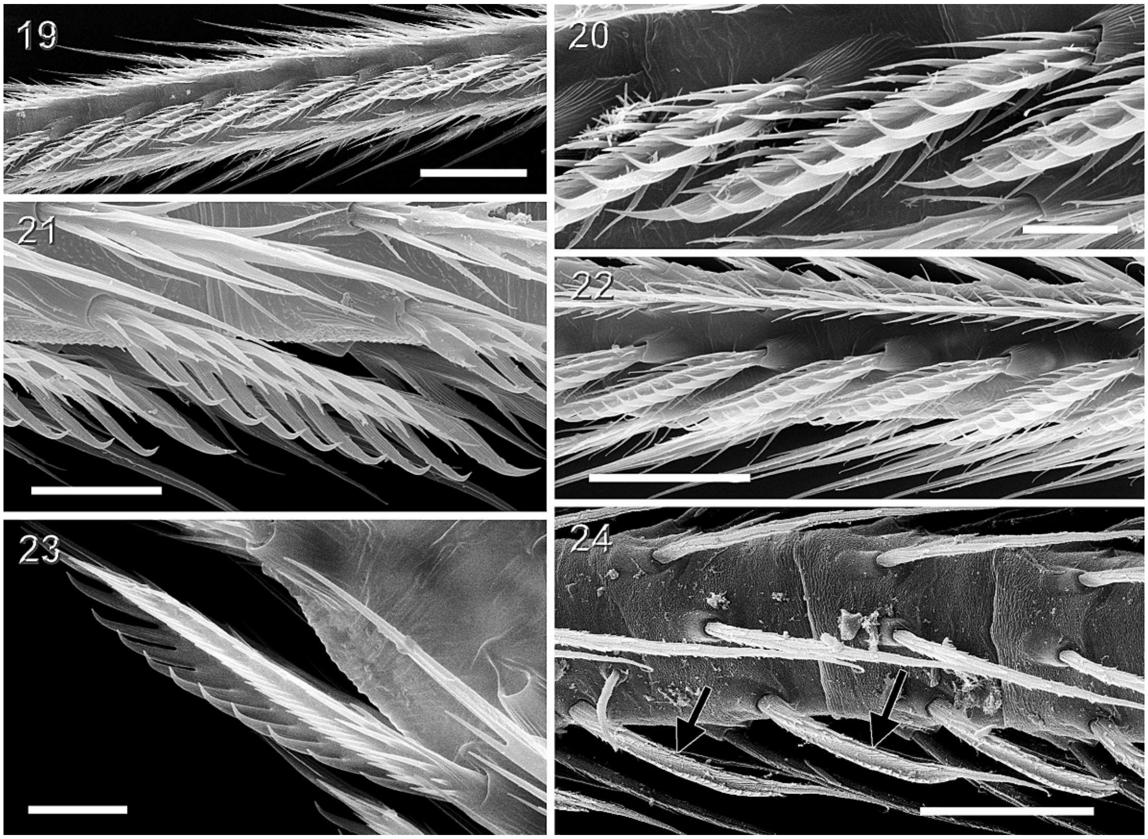


Figures 13–18.—Hairs on tarsus 4, ''holocnemines.'' 13. *Hoplopholcus minotaurus*, female left tarsus 4, prolateral; 14. *Smeringopina pulchra*, female tarsus 4, ventral; note two rows of comb-hairs; 15. *Physocyclus globosus*, female right tarsus 4, prolateral; 16. *Trichocyclus nullarbor*, female left tarsus 4, prolateral; 17, 18. *Artema atlanta*, female left tarsus 4, prolateral. Scale lines: 20 µm (14, 16, 18), 40 µm (13), 50 µm (15), 70 µm (17).

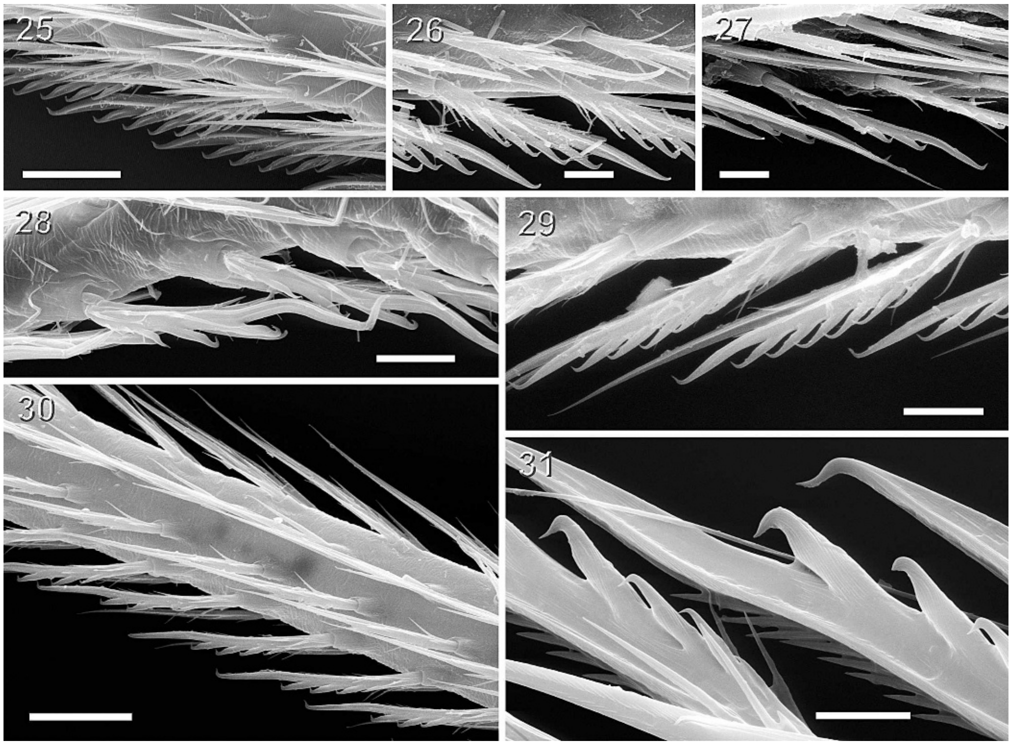
grasp silk in functional correlation with the median claw in many spider families (the ''accessory claws'' of Nielsen 1932; see figures 14–16 in Foelix 1970). This scenario is speculative, but recruitment of structures functioning in a closely related context appears more parsimonious than *de novo* modification of mechanoreceptors unrelated to silk manipulation. The similarity between comb-hairs and accessory claws has also been noted in theridiids (Agnarsson 2004: 591).

Comb-hair function.—Previous data (Kirchner & Opderbeck 1990) as well as our data on details of comb-hair function are very preliminary. Obviously, our method of spraying spiders during wrap attack, the transfer into ethanol, and the subsequent manipulations preparing the object for the SEM minimize the chances for the silk lines to remain in functional contact with the comb-hairs. However, we see no reason to assume that the hair running through the notch in Fig. 31 is just an artifact. We hypothesize that this is at least close to the actual method of contact, but we are aware that most questions in this regard remain unanswered: Why does a sticky silk line not adhere permanently to a comb-hair? How does a comb-hair ''grasp'' a line to pull it out of the spigot? What exactly happens when a silk line is released by the comb-hair? What is the function of the additional rows of branches in the *Belisana*-type of hair? The size of the structures involved, as well as the high amplitude and speed of the wrapping movements (usually $<$ 0.5 s per cycle in *P. phalangioides*; Jackson & Brassington 1987; Kirchner & Opderbeck 1990) makes this appear a rather daunting challenge for future research.

Given this relative lack of detailed knowledge on comb-hair function, alternative functional interpretations must be considered. Pholcids and theridioids share a further, unusual character, i.e., the use of gumfoot lines (for pholcids see Japyassú & Macagnan 2004). However, not all pholcids studied use gumfoot lines while all pholcids studied use ss-wrap. In addition, pholcids apply the sticky droplets to the gumfoot line when returning to the sheet (Japyassú & Macagnan 2004), which means that the fourth legs do not



Figures 19–24.—Hairs on tarsus 4, ‘‘basal’’ Pholcines. 19, 20. *Paramicromerys scharffi*, female right tarsus 4, prolateral-ventral; 21. *Belisana ketambe* Huber 2005, female left tarsus 4, prolateral; 22. *Buitinga asax*, male right tarsus 4, prolateral; 23. *Spermophora senoculata*, female right tarsus 4, prolateral; 24. *Spermophora kerinci* Huber 2005, female left tarsus 4, prolateral. Arrows point to selected comb-hairs. Scale lines: 10 µm (20, 21, 23), 30 µm (24), 40 µm (19, 22).



Figures 25–31.—Hairs on tarsus 4, *Pholcus* and close relatives. 25. *Micropholcus fauroti*, male right tarsus 4, prolateral; 26. *Uthina luzonica*, female left tarsus 4, prolateral; 27. *Calapnita phyllicola*, male left tarsus 4, prolateral; 28. *Micromerys daviesae*, male left tarsus 4, prolateral; 29. *Pehrforsskalia conopyga*, male right tarsus 4, prolateral; 30. *Panjange mirabilis*, female right tarsus 4, prolateral; 31. *Pholcus phalangioides*, female tarsus 4 hairs with silk line freeze-fixed during wrap-attack. Scale lines: 10 µm (26-29, 31), 20 µm (25), 30 µm (30).

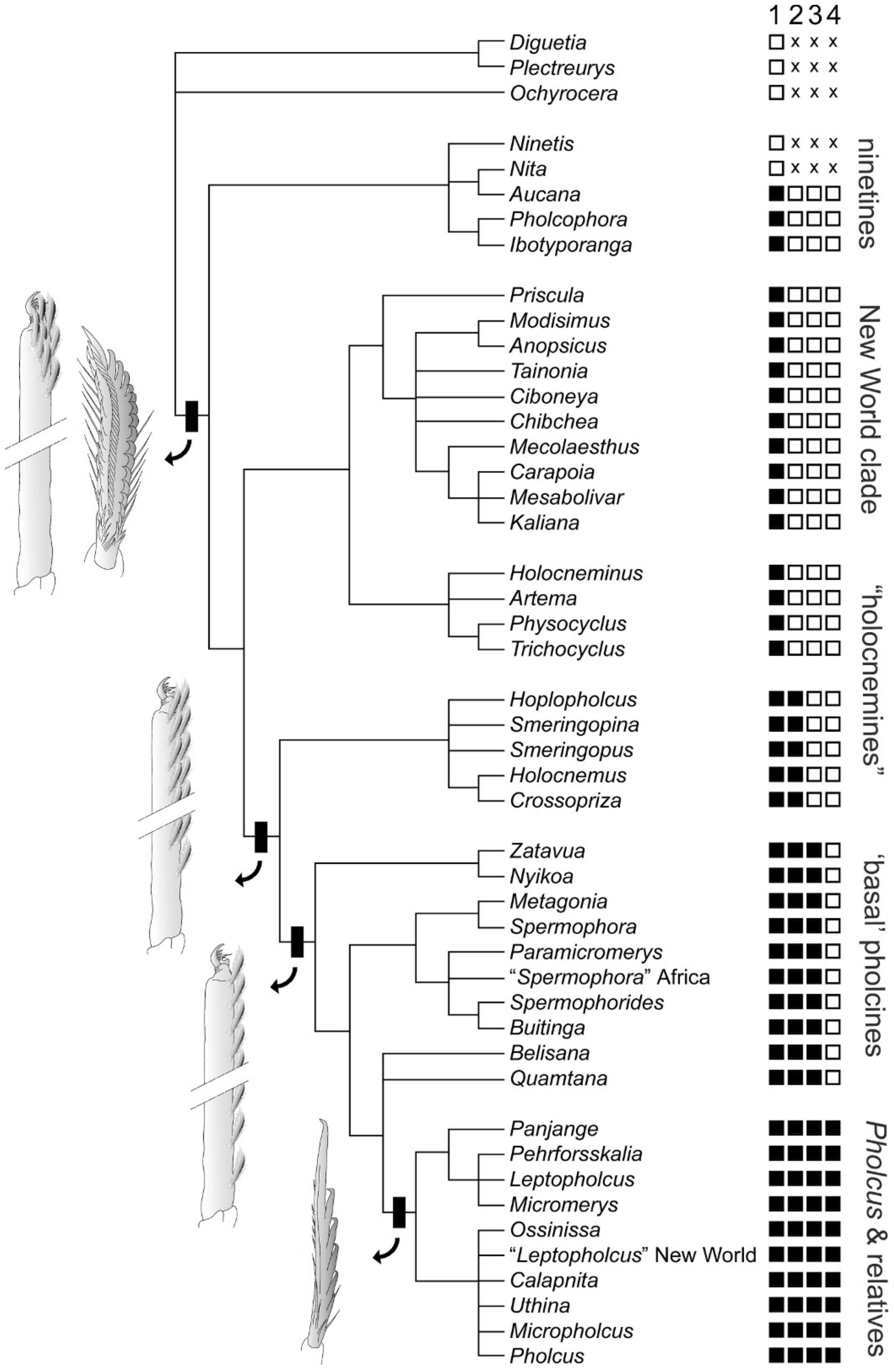


Figure 32.—Cladogram of Pholcidae derived from various previous works using molecular and morphological characters (Huber 2000, 2001, 2003a, b, c, 2005a, b; Bruvo-Mađarić et al. 2005; Huber & El Hennawy 2007; Astrin et al. 2007; B.A. Huber unpublished data on *Pholcus* and close relatives). Only taxa studied herein are included (except for *Khorata* whose position within pholcines remains obscure). Hashmarks and figures at the left indicate hypothesized evolutionary changes: Origin of comb hairs (complex, in distal patches; see text for apparent secondary reduction in Old World ninetines); Elongation of patch to cover most or entire tarsus length; Reduction to a single ventral row; Simplification of comb-hair. Character states for each taxon are shown at the right: (1) Comb-hair absent vs. present; (2) Distal patch vs. long row(s); (3) Patch or two rows vs. single row; (4) Complex vs. simple comb-hair.

manipulate sticky silk during gumfoot production (in contrast to ss-wrap). We interpret this as evidence for the hypothesis that comb-hairs function in the context of ss-wrap rather than gumfoot production.

We would like to point out that a similar unsolved problem exists in the analogous case of cribellate silk that is pulled out by a comb of hairs on the fourth metatarsus in cribellate spiders. These hairs are usually strongly sculptured, and in some species they carry multiple combs with over 3000 teeth per hair (Foelix & Jung 1978 on *Hypochilus thorelli* Marx 1888). How exactly the silk is grasped and released by the hairs seems to remain unknown.

Comparison with theridiids.—Theridiid comb-hairs have been known for a long time, and numerous illustrations of a variety of taxa exist in the literature (e.g., Kropf 1990; Agnarsson 2004; Knoflach & Pfaller 2004). However, we know of no systematic effort to summarize and characterize the morphological variation within the family. The only exception (Kasal 1997) appears rather incomprehensive, lacking detail, and based on purely speculative evolutionary reasoning. Published SEM photographs show that there is considerable variation of comb-hairs among theridiid taxa (but the view is often not given), and that in some taxa the hairs are quite similar to those of certain pholcids. Theridiid comb-hairs seem to be consistently spread over the entire length of the tarsus. Like in pholcids, no data on the functional details are available.

Comb-hairs in other taxa.—Comb-hairs have been reported in a number of other taxa, but the functional context is different from that in pholcids and theridioids in most or all of them. The homology of synotaxid comb-hairs with those of theridioids remains unclear. Agnarsson (2003) writes that the ''serrated setae on the fourth tarsus of *Synotaxus* ...share little similarity with the theridiid comb,'' and concludes that these are ''superficial similarities.'' In a cladistic analysis of theridiids and relatives by the same author (Agnarsson 2004), the data suggest that comb-hairs are a synapomorphy of the ''spineless femur clade,'' a group including theridioids plus synotaxids and cyatholipids. The observation by Coddington (1986: 335) of ss-wrap in *Synotaxus* strengthens the idea that synotaxid comb-hairs, even though morphologically different and not present in all species (Exline & Levi 1965) are homologous to those of theridioids.

In the anapid *Comaroma simoni* Bertkau 1889, comb-hairs have been found on all tarsi. They appear to function in the context of cleaning (Kropf 1990). Very distinctive comb-hairs have been found on the third legs of certain *Mesabolivar* (Pholcidae) species (E. Machado, pers. comm.). Their function remains unknown, but there might be some correlation with the sexually dimorphic modification of male third legs (thickened femora) in certain *Mesabolivar* species. Thickened male third femora also occur in some other pholcid genera (Huber 1994, 2000: p. 17) but the third tarsal hairs of these taxa remain unstudied.

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