

LARVAL CHAETOTAXY IN WOLF SPIDERS (ARANEAE, LYCOSIDAE): SYSTEMATIC INSIGHTS AT THE SUBFAMILY LEVEL

Beata Tomasiewicz: Zoological Institute, Department of Biodiversity and Evolutionary Taxonomy, Przybyszewskiego 63/77, 51–148 Wrocław, Poland. E-mail: beatatomas@interia.pl

Volker W. Framenau: Department of Terrestrial Invertebrates, Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia.

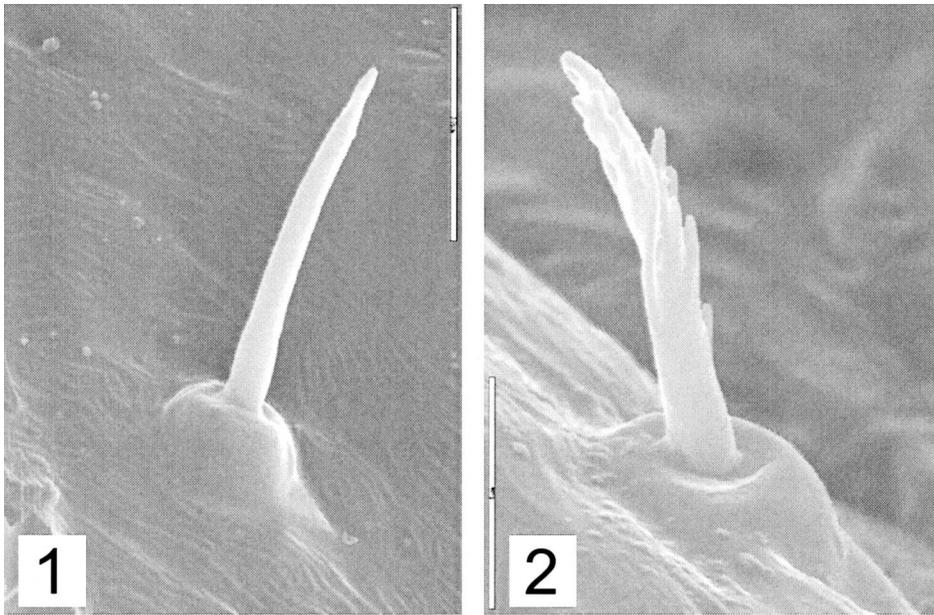
ABSTRACT. Studies into the systematics of wolf spiders have mainly employed morphological characters of adult spiders, in particular features of the male and female genitalia, and more recently mitochondrial DNA sequence data. However, there is still no established phylogenetic framework for the Lycosidae, even at the subfamily level. This study uses a novel morphological character set, the chaetotaxy of lycosid larvae (presence and arrangement of setae and slit organs), to infer systematic information on seven species of wolf spiders that are currently listed in three subfamilies: Lycosinae [*Alopecosa pulverulenta* (Clerck 1757), *Hogna antelucana* (Montgomery 1904), *Rabidosa rabida* (Walckenaer 1837), *Trochosa ruricola* (DeGeer 1778)], Piratinae [*Hygrolycosa rubrofasciata* (Ohlert 1865), *Pirata hygrophilus* (Clerck 1757)], and Sosippinae (*Sosippus californicus* Simon 1898). Cheliceral and tarsal (legs I and II) chaetotaxic patterns of the first postembryo showed equivalent chaetotaxic complexes amongst all species but revealed considerable differences between representatives of the three subfamilies. *Sosippus californicus* showed the most complex pattern and *P. piraticus* the most reduced arrangement. In addition, it casts doubt on the previous listings of *H. rubrofasciata* in either the Lycosinae or Piratinae, as its chaetotaxic setae arrangement was more similar to *S. californicus* than to any other species investigated here.

Keywords: Larval stages, chaetotaxic complex, Lycosinae, Piratinae, Sosippinae

Chaetotaxy, the presence and arrangement of setae and other sensory structures on the integument of arthropods, has been widely used for systematic and taxonomic studies in a variety of groups, including insects (e.g. Alarie & Watts 2004) and arachnids such as mites (Tuzovsky 1987; Griffith et al. 1990) and pseudoscorpions (e.g. Chamberlin 1931; Harvey 1992). In contrast, investigations into the chaetotaxy of spiders are comparatively rare and have focused mainly on trichobothrial patterns. These have been argued to be a suitable feature in higher level systematics (Lehtinen 1980; Scioscia 1992). They may also serve as an important tool in identification at the species level. For example, the position of the metatarsal trichobothrium has been used as an essential character in the identification of central European Micryphantinae Bertkau 1872 (Wiehle 1960; Heimer & Nentwig 1990).

There is a considerable difference between the chaetotaxic pattern of immature and adult

arthropods and larval chaetotaxy has been argued to represent an excellent character set for systematic studies (Pomorski 1996). Larval morphology is of particular interest in holometabolic insects such as beetles (Kilian 1998; Borowiec & Świętojańska 2003) and butterflies (Kitching 1984, 1985) as different expressions of the same genotype can complement the morphological characters of adults (Alarie & Watts 2004; Grebennikov 2004; Ashe 2005). However, larval chaetotaxy has also been useful in phylogenetic and taxonomic studies of arthropods with gradual larval development such as springtails, mites and pseudoscorpions (Nayrolles & Betsch 1993; Pomorski 1996; Griffith et al. 1990; Harvey 1992). Early stages of development may last for only a short period of time, which in many cases eliminates the development of distinct adaptive traits. In addition, the morphology of juveniles is less variable and complex than that of adults (Pomorski 1996).



Figures 1, 2.—Larval setae of wolf spiders. 1. Seta form [position: apical/etc leg/chelicera etc] of [species]; 2. Serrated seta from [position: apical/etc., leg/chelicera etc.] of [species]. Scale bar: 10 μm (Fig. 1), 5 μm (Fig. 2).

Studies on chaetotaxic structures in immature spiders are rare and initially focused on trichobothrial patterns (Emerit 1964). A recent study of the linyphiid spider *Bathyphanthes eumenis* (L. Koch 1879) included all sensory structures of the protonymph and showed that the arrangement of sensory organs such as setae, trichobothria and slit organs was constant in all examined specimens and may have the potential to serve in the identification of spiders at the generic and species level (Rybak & Pomorski 2003). The nomenclature of the chaetotaxic patterns developed for *B. eumenis* was subsequently used in a detailed comparative study including the wolf spider *Trochosa ruricola* (DeGeer 1778) (Lycosidae) (Rybak & Tomasiewicz 2005). Although this study showed considerable differences in chaetotaxic pattern between both species, some body parts showed very similar setae distribution, which suggested homology for a large number of chaetotaxic complexes.

Despite recent investigations into the systematics of wolf spiders, there is still no accepted phylogenetic framework for the Lycosidae, even at the subfamily level (e.g. Dondale 1986; Zyuzin 1993; Vink et al. 2002). This problem can be attributed to a lack of well-

defined morphological characters that could classify and separate particular genera and subfamilies. However, there appears to be a consensus that web-building wolf spiders, such as the genera *Sosippus* Simon 1888 (sheet-web) and *Pirata* Sundevall 1833 (tube-shaped retreat) represent more ancient evolutionary lines in comparison to genera within the Lycosinae Simon 1898 (*Trochosa* C.L. Koch 1847, *Alopecosa* Simon 1885, *Rabidosa* Roewer 1960 and *Hogna* Simon 1885) that are considered representatives of more recent evolutionary lineages (Dondale 1986; Zehethofer & Sturmbauer 1998; Vink et al. 2002).

The genus *Hygrolycosa* Dahl 1908 was formerly placed in the Lycosinae along with, amongst others, *Alopecosa*, *Hogna* and *Trochosa* (Dondale 1986). However, more recently, it was listed in a separate subfamily, Piratinae Zyuzin 1993, based on the shape and location of the embolus and the functional conductor in the male pedipalp (Zyuzin 1993). Current molecular evidence suggests that *Hygrolycosa* is a sister taxon to *Aulonia albimana* (Walckenaer 1805) in a clade that also includes *Pirata*, *Venonia* Thorell 1894 (Venoniinae Lehtinen & Hippa 1979) and *Xeroly-*

Table 1.—Nomenclature of chaetotaxic complexes on the larval integuments of *A. pulverulenta*, *H. antelucana*, *H. rubrofasciata*, *P. hygrophilus*, *R. rabida*, *S. californicus* and *T. ruricola*.

Abbreviation	Chaetotaxic complex	Illustrations
Chelicerae		
Ch _{DA}	dorsal apical complex	Figs. 1–4
Ch _{DM}	dorsal median complex	Figs. 1–4
Ch _{VAM}	ventral apico-median complex	Figs. 5–8
Ch _{VM}	ventral median complex	Figs. 7–8
Tarsi I and II		
T _{DA}	dorsal apical complex	Fig. 9
T _{DAI} , T _{DAII} ...	first, second, ... dorsal apical complex	Figs. 10–11
T _{DM}	dorsal median complex	Fig. 9
T _{DMI} , T _{DMII} ...	first, second, ... dorsal median complex	Figs. 10–13
T _{DP}	dorsal proximal complex	Figs. 10–13
T _{VAI} , T _{VAIL} ...	first, second, ... ventral apical complex	Figs. 12–14
T _{VM}	ventral median complex	Fig. 12
T _{VMI} , T _{VMI} ...	first, second, ... ventral medial complex	Figs. 13–14
T _{VP}	ventral proximal complex	Figs. 13–14

cosa Dahl 1908 (Evippinae Zyuzin 1985) (N. Murphy et al. in press).

The main objective of this study was to evaluate the significance of larval chaetotaxic patterns for systematic analyses in wolf spiders. More specifically, we used the ambiguous subfamily placement of *H. rubrofasciata* to assess its previous listings in either the Lycosinae or Piratinae by including representatives of these subfamilies in our comparative analysis.

METHODS

We analyzed the larval stages of seven species of wolf spiders currently listed in three different subfamilies: Lycosinae [*Alopecosa pulverulenta* (Clerck 1757), *Hogna antelucana* (Montgomery 1904), *Rabidosa rabida* (Walckenaer 1837), and *Trochosa ruricola* (DeGeer 1778)], Piratinae [*Hygrolycosa rubrofasciata* and *Pirata hygrophilus* (Clerck 1757)], and Sosippinae (*Sosippus californicus* Simon 1898). We obtained immature stages through laboratory colonies (*T. ruricola*, *A. pulverulenta*, *H. rubrofasciata* and *P. hygrophilus*) or loan and donation of material from overseas collections (*H. antelucana*, *R. rabida* and *S. californicus*).

Overall, we studied 64 specimens of *T. ruricola*, 10 specimens each of *H. rubrofasciata* and *P. hygrophilus* and 5 specimens each of *A. pulverulenta*, *H. antelucana*, *R. rabida*, and *S. californicus*. There was no intraspecific var-

iation in regard to the number of structures within chaetotaxic complexes, which allowed analysis of data without statistical consideration of variation.

Specimens were transferred to 5% KOH and cleared in distilled water. Subsequently, they were placed in chloramphenol and mounted in Swan medium (20 g distilled water, 60 g chloral hydrate, 15 g gum arabic, 3 g glucose, 2 g glacial acetic acid). All slides were examined under a phase contrast microscope (Nikon Eclipse E 600) with a drawing attachment. Scanning electron microscope (SEM) photographs were taken with a JEOL JSM-5800 LV at 15kV after spray-coating the specimen with gold. Voucher specimens of the species examined were lodged at the Museum of Natural History, Wrocław (*A. pulverulenta*, *P. hygrophilus*, *H. rubrofasciata*) and the California Academy of Sciences, San Francisco (*H. antelucana*, *R. rabida*, *S. californicus*).

Larval stages.—We investigated the first immature stage that possesses chaetotaxic structures on the integument, i.e. the first postembryo. These young spiders develop inside the egg-sac followed by the protonymph, which abandons the egg-sac (Vachon 1957). Vachon (1957) proposed the term ‘larva’ for the first postembryo, which corresponds to ‘stage D’ (Holm 1940), ‘préjuvenilé (Ji 1)’ (Canard 1987), ‘larva “setose stage”’ (Hallas 1988), and ‘IV instar’ (Galiano 1991). Con-

sequently, all references to 'larvae' or 'larval' in this study refer to the first postembryo.

Chaetotaxic structures.—Although numerous chaetotaxic structures such as spines, trichobothria, proprioceptors in the form of hair plates, and chemoreceptors in the form of tarsal organs, and taste hairs exist in spiders (Foelix 1996; Rybak & Pomorski 2003), this study deals with setae and slit organs because only these structures were observed on the larval integument. In adult spiders, setae are triply innervated hair-like structures that serve purely mechanical tasks (tactile receptors). They consist of a long exocuticular shaft of variable shape (including serrated and plumose), which is suspended in a slipper-shaped socket in which it can move (Rybak & Pomorski 2003). In contrast, spines are rigid structures that are regarded as hemolymph pressure receptors (Foelix & Chu-Wang 1973). In immature spiders, it is difficult to distinguish between spines and setae as the socket and the setae are generally not fully developed (Figs. 1, 2), although different types of setae may exist (Bond 1994). Consequently, within the scope of our study, we do not differentiate between setae and spines. Slit organs occur both in adult and larval spiders. They sense mechanical stress in the exoskeleton caused by vibrations, gravity or the spider's own movement and occur singly ('slit sensillae') or in groups where slits run parallel to each other ('lyriform organs') (Foelix 1996). In this study, the chaetotaxic structures on larval chelicerae and tarsi were grouped into distinct complexes. The nomenclature of these complexes follows Rybak & Pomorski (2003) and Tomasiewicz & Rybak (2005) (see also Table 1).

RESULTS

There were considerable differences in the number of chaetotaxic structures on the larval bodies of the investigated species, which allowed separating them into two main groups (Tables 2 & 3). While *A. pulverulenta*, *H. antelucana*, *P. hygrophilus*, *R. rabida* and *T. ruricola* possessed chaetotaxic structures only on the chelicerae, labium, maxillae, legs and pedipalps, *H. rubrofasciata* and *S. californicus* exhibited chaetotaxy on all body parts including sternum, carapace, abdomen and spinnerets. Chelicerae and the tarsi of legs I and II showed distinct chaetotaxic patterns, which

allowed a comparison between species and genera. These structures were most complex in *S. californicus* (Figs. 6, 10, 13, 16) and *H. rubrofasciata* (Figs. 5, 9, 12, 15) and most reduced in *P. piraticus* (Figs. 3, 7, 11, 14).

Chelicerae dorsal.—All species possessed the apical complex Ch_{DA} . The number of setae within this complex differed between *P. hygrophilus* (four setae; Fig. 3), a group comprising *T. ruricola*, *A. pulverulenta*, *R. rabida*, and *H. antelucana* (seven setae; Fig. 4) and a group with *H. rubrofasciata* and *S. californicus* (10 setae; Figs. 5, 6). *Hygrolycosa rubrofasciata* and *S. californicus* had an additional median complex Ch_{DM} that consisted of three setae, which were long in *S. californicus* and very short in *H. rubrofasciata*. All species had one slit sensilla in the median section of the chelicerae and two slit sensillae apically (Figs. 3–6).

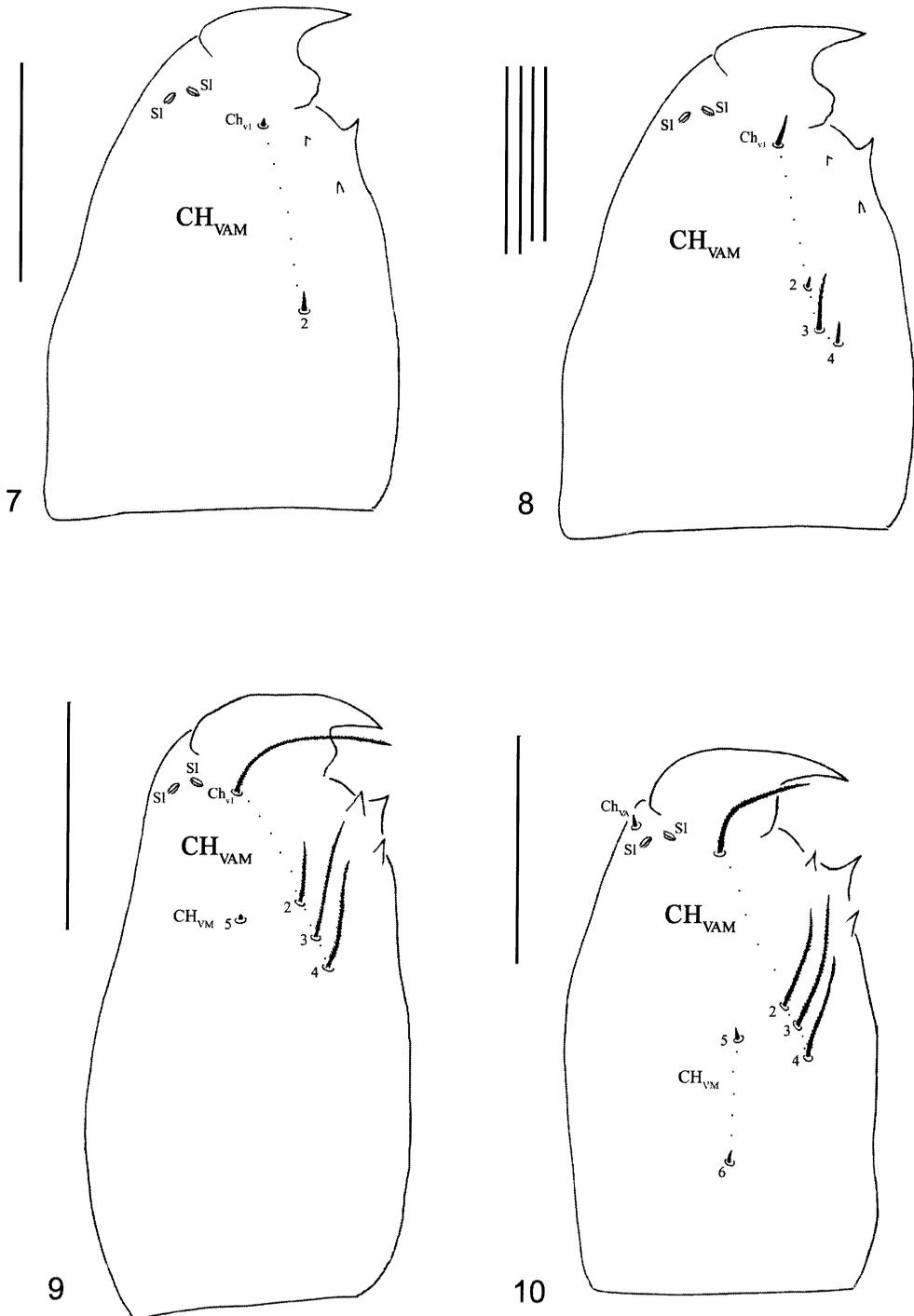
Chelicerae ventral.—All species showed an apico-median complex Ch_{VAM} that consisted of one or two setae in *P. hygrophilus* (Fig. 7), and four setae in all other species (Figs. 8–10). *Hygrolycosa rubrofasciata* (Fig. 9) and *S. californicus* (Fig. 10) possessed a further structure Ch_{VM} , consisting of a single seta in *H. rubrofasciata* and two setae in *S. californicus*. The latter species showed an additional apical seta Ch_{VA} that did not exist in any of the other lycosids. All species possessed two slit sensillae apically (Figs. 7–10).

Tarsi of legs I and II dorsal.—All species examined showed two similar complexes, T_{DA} and T_{DM} in *T. ruricola*, *H. antelucana*, *R. rabida*, *A. pulverulenta*, and *P. hygrophilus* (Fig. 11), corresponding to T_{DAIII} and T_{DMIV} in *H. rubrofasciata* (Fig. 12) and T_{DAII} and T_{DMIV} in *S. californicus* (Fig. 13). *Hygrolycosa rubrofasciata* (Fig. 12) and *S. californicus* (Fig. 13) showed seven more complexes in which the apical ones had a larger number of setae in *S. californicus*. All lycosids showed slit sensillae located laterally in the median part of the tarsi (Figs. 11–13).

Tarsi of legs I and II ventral.—All species showed three identical complexes, T_{VAI} , T_{VAII} , and T_{VM} in *T. ruricola*, *H. antelucana*, *A. pulverulenta* and *P. hygrophilus* (Fig. 14), corresponding to T_{VAI} , T_{VAIII} , and T_{VMI} in *H. rubrofasciata* and *S. californicus* (Figs. 15–16). The complex T_{VMI} consisted of three setae in *H. rubrofasciata* (Fig. 15) (as the equivalent complex T_{VM} in the other above-men-



Figures 3–6.—Chaetotaxic pattern on dorsal side of the chelicerae in wolf spider larvae: 3. *Pirata hygrophilus*; 4. *Alopecosa pulverulenta*, *Hogna antelucana*, *Trochosa ruricola*, *Rabidosia rabida*; 5. *Hygrolycosa rubrofasciata*; 6. *Sosippus californicus*. Scale bar: 0.1 mm. Multiple scale bars in Fig. 4 reflect the comparative scale of the species in the given sequence.



Figures 7–10.—Chaetotaxic pattern on ventral side of the chelicerae in wolf spider larvae: 7. *Pirata hygrophilus*; 8. *Alopocosa pulverulenta*, *Hogna antelucana*, *Trochosa ruricola*, *Rabidosia rabida*; 9. *Hygrolycosa rubrofasciata*; 10. *Sosippus californicus*. Scale bar: 0.1 mm. Multiple scale bars in Fig. 8 reflect the comparative scale of the species in the given sequence.

tioned lycosids), but included four setae in *S. californicus* (Fig. 16). *Sosippus californicus* and *H. rubrofasciata* showed six additional complexes (T_{VAII} , T_{VC} , T_{VMII} , T_{VMIII} , T_{VMIV} , T_{VP} in *H. rubrofasciata* and T_{VAII} , T_{VMII} , T_{VMIII} , T_{VMIV} , T_{VMV} , T_{VP} in *S. californicus* (Figs. 15, 16). Although these two species showed the most similar chaetotaxic patterns, there are complexes (T_{VMIV} , T_{VC} in *H. rubrofasciata* and T_{VMIV} , T_{VMV} in *S. californicus*) (Figs. 15, 16) among which it is difficult to establish homology. Both species showed slit sensillae situated medially near the apical part of the tarsi, which were absent in all other species (Figs. 14–16).

DISCUSSION

Our analysis of chaetotaxic patterns in wolf spiders showed distinct and regular complexes for all species examined. These complexes appear to be similar to the arrangement in other spider families such as the Linyphiidae (Rybak & Pomorski 2003), which suggests that larval chaetotaxy may serve as a very useful character set in systematic studies if homologies can be established on a higher taxonomic level. However, there was no difference of chaetotaxic patterns among any of the species currently included in the subfamily Lycosinae. In contrast to other arthropods, in particular insects (e.g. Deruaz et al. 1991; Alarie & Watts 2004), larval chaetotaxy does not seem to be suitable for the identification of taxa below subfamily level in wolf spiders.

There were significant differences in the number of complexes of cheliceral and tarsal setae and the number and size within these complexes. *Sosippus californicus* showed the most complex pattern along with *H. rubrofasciata* that differed only in the absence of two setae on the ventral side of the chelicerae, the absence of the complex equivalent to T_{VMIV} in *S. californicus*, and a reduction in the number of setae in the apical and proximal complexes of the tarsi. On the other hand, all four species of Lycosinae and *P. piraticus* showed very similar setal arrangements (Table 2). Here, chaetotaxy was heavily reduced in comparison to *Sosippus* and *Hygrolycosa*, in particular in regard to the tarsal setae. *Pirata piraticus* had the lowest number of setae as complex CH_{DA} and CH_{VM} had two setae less each than the equivalent complexes in the Lycosinae. This separation into two major groups, supported

by the overall distribution of chaetotaxic complexes on the bodies of the spiders (Table 3), does not reflect current phylogenetic hypotheses for wolf spiders. Morphological (Dondale 1986) and molecular (Zehethofer & Sturmbauer 1998; Vink et al. 2002; Murphy et al. in press) phylogenies consider the Lycosinae as the most derived lineage of wolf spiders, whereas the Piratinae and Sosippinae are thought to represent more basal evolutionary lines.

Although we included a wide range of taxa from different currently recognized subfamilies our study is ambiguous in regards to the plesiomorphic condition for larval chaetotaxic structures. Both *Pirata* and the sheet-web building *Sosippus* are thought to represent basal lineages in the evolution of wolf spiders but they differ considerably in their larval chaetotaxy. Preliminary studies on the chaetotaxy of *Pisaura mirabilis* (Clerck 1757) representing the Pisauridae, a putative sister taxon of the Lycosidae (Dondale 1986; Griswold 1993), show considerably reduced chaetotaxic patterns (Tomasiewicz unpub. data) supporting *P. hygrophilus* to display the plesiomorphic state. In this case, and in combination with current phylogenetic hypotheses (Murphy et al. in press), an increase in chaetotaxic structures has evolved twice within our sampled taxa, in *Sosippus* and *Hygrolycosa*.

The chaetotaxic pattern of *H. rubrofasciata* differs considerably from all other lycosine and piratinae species examined, the two subfamilies where it was previously listed (Dondale 1986; Zyuzin 1993) and our study suggests an alternative placement within the Sosippinae. However, current molecular data place *H. rubrofasciata* in a basal lineage within in the Lycosidae, close to the Venoniinae, Piratinae and Evippinae (Murphy et al. in press), providing support for Zyuzin's (1993) placement of the genus and at the same time rejecting chaetotaxic patterns as informative for the subfamilial placement of *Hygrolycosa*.

This preliminary study shows that larval chaetotaxy may provide some additional morphological evidence that bears phylogenetic information in spiders although some discrepancies with common tenets of current phylogenetic hypotheses in wolf spiders exist. It is not possible to distinguish species or even

Table 2.—Number of setae per chaetotaxic complex on the chelicerae and tarsi of leg II and III of *A. pulverulenta*, *H. antelucana*, *H. rubrofasciata*, *P. hygrophilus*, *R. rabida*, *S. californicus* and *T. ruricola*.

	<i>A. pulverulenta</i>			
	<i>H. antelucana</i>			
	<i>P. hygrophilus</i>	<i>R. rabida, T. ruricola</i>	<i>H. rubrofasciata</i>	<i>S. californicus</i>
Ch _{DA}	7	7	10	10
Ch _{DM}	—	—	3	3
Ch _{VAM}	2	4	4	4
Ch _{VM}	—	—	1	2
T _{DA}	3	3	—	—
T _{DAI}	—	—	5	5
T _{DAII}	—	—	2	3
T _{DAIII}	—	—	3	2
T _{DM}	2	2	—	—
T _{DMI}	—	—	4	4
T _{DMII}	—	—	3	3
T _{DMIV}	—	—	2	2
T _{DMV}	—	—	2	2
T _{DP}	—	—	2	2
T _{VAI}	2	2	2	2
T _{VAII}	—	—	4	4
T _{VAIII}	—	—	3	3
T _{VM}	3	3	—	—
T _{VMI}	—	—	3	4
T _{VMI}	—	—	4	5
T _{VMI}	—	—	3	2
T _{VMI}	—	—	4	3
T _{VMI}	—	—	—	3
T _{VC}	—	—	2	—
T _{VP}	—	—	4	4

tain only a limited amount of information since a reduction of structures may have easily occurred in multiple evolutionary lines. Distinguishable morphological categories of setae exist in wolf spider larvae, for example smooth and serrated forms (Figs. 1, 2). Future research could explore an expanded character set and subsequently code it as morphological matrix for a phylogenetic analysis similar to some studies of insects (e.g., Alarie & Watts 2004; Ashe 2005). This could then be incorporated in an exhaustive morphological and molecular dataset for higher phylogenetic analysis in spiders.

The analysis of larval chaetotaxy may bear considerable importance in interpreting structures of mature spiders, in particular during character polarization as part of a phylogenetic analysis (ontogenetic criterion, see Hennig 1966; Nelson 1978; Mabee 2000). For example, the study of setal arrangement during postembryonic development has been helpful in determining the phylogenetic migration of

homological chelal trichobothria in pseudoscorpions (Harvey 1992) and the setal arrangement in astigmatid mites (Griffith et al. 1990).

Currently, it remains difficult to acquire larval material for morphological studies since larvae and juveniles are often discarded during the collection of spiders, and, if collected, the material may not represent a suitable developmental stage for comparative studies. However, if larval chaetotaxy can be established as an important morphological tool in phylogenetic studies of spiders, the collection and preservation of spider larvae may receive much stronger support.

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Table 3.—Presence of chaetotaxic structures on the larval bodies of *A. pulverulenta*, *H. antelucana*, *H. rubrofasciata*, *P. hygrophilus*, *R. rabida*, *S. californicus* and *T. ruricola*. sl – slit sensillae, ly – lyriform organs.

	<i>A. pulverulenta</i> <i>H. antelucana</i> , <i>P. hygrophilus</i> <i>R. rabida</i> , <i>T. ruricola</i>	<i>H. rubrofasciata</i> <i>S. californicus</i>
Chelicerae	setae, sl	setae, sl
Labium	setae	setae
Maxillae	setae	setae
Sternum	—	setae, sl
Carapace	—	setae
Pedipalps	setae, ly, sl	setae, ly, sl
Legs	setae, ly, sl	setae, ly, sl
Abdomen	—	setae
Spinnerets	—	setae

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