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Comparative morphology of pretarsal scopulae in eleven spider families

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ABSTRACT

Many wandering spiders bear attachment pads (scopulae) on their tarsi, consisting of hierarchically-branching adhesive setae. Amongst spider families and even species, these show remarkable differences in morphology. Using scanning electron microscopy, the scopula microstructure of sixteen spider species was described, with the focus on pretarsal scopulae (claw tufts). Area and shape of the claw tuft, seta and setule density, as well as seta and spatula dimensions were analysed and compared. Claw tufts of the majority of species studied show a similar gradient in size and shape from anterior to posterior legs: the dimension of pads increases, while setal density decreases. Commonly, there is also a gradient of both the seta and spatula size within the claw tuft: Setae become larger from the proximal to the distal part of the pad, and spatulae size increases in the same direction at the level of individual seta. Often, different hierarchical levels of claw tuft organisation are differently expressed in different species: Species with lower setal density usually have broader setae. Smaller spatula size often implicates higher setule density. Evolutionary and ecological aspects of the scopula origin are discussed.

1. Introduction

A wide-spread morphological feature of terrestrial arthropods is the presence of adhesive setae, cuticular structures that provide dynamic attachment to various surfaces. These structures have evolved independently several times, indicating their enormous efficiency and biological success (Scherge and Gorb, 2001; Beutel and Gorb, 2001). In wandering spiders, the complexity of the adhesive apparatus has reached a superior level among arthropods: specialized hierarchically-branched setae are organized in dense arrays, called scopulae. We speak about the hierarchy, if the cuticle protuberances are covered with smaller protuberances. Scopulae are located on both ventral and lateral parts of the tarsus and metatarsus. Strongly-specialised distal scopulae, so-called claw tufts situated at the tip of the tarsus, play a major role in attachment during locomotion. Their microstructure was described for the first time by Homann (1957): The adhesive setae are flattened and covered with hundreds of microtrichia (called setules) on their ventral side. Each setula ends in a broadened plate-like structure, the spatula. It can be assumed that these setae are modified tactile hairs, which sometimes still are supplemented by a single sensory cell (Foelix et al., 1984).

Beside the claw tufts, scopulae are also often present on the anterio- and posterio-lateral parts of the tarsi and metatarsi in the anterior legs. In contrast to those in the claw tuft, the adhesive sides of setae in these parts are distally-orientated (Niederegger and Gorb, 2006) and can be activated through the erection of hairs, caused by increasing hemolymph pressure (Rovner, 1978; Foelix et al., 1984). Leg scopulae mainly play a role in prey capture, when large and/or dangerous prey has to be secured and held away from the body (Rovner, 1978; Foelix et al., 1984; Pekár et al., 2011). They also might support the spider's body, while resting on steep surfaces and climbing over edges (Niederegger and Gorb, 2006).

Depending on its physical mechanism of adhesion, the spider's body dimensions, the ecological and ethological demands, and its phylogenetic origin, the scopula can be highly diverse in various spider species. Whereas the variety of attachment devices in insects is well covered by numerous publications (for reviews, see Beutel and Gorb, 2001; Gorb, 2001; Gorb and Beutel, 2001), there are only a few descriptions of adhesive systems of some individual species of spiders (Homann, 1957; Foelix and Chu-Wang, 1975; Hill, 1977; Roscoe and Walker, 1991; Kesel et al., 2003; Moon and Park, 2009; Foelix and Erb, 2011). In the systematic literature claw tufts are widely used as a character, whereas a detailed morphological description and understanding of the functional mechanism is

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lacking (Homann, 1975; Forster and Platnick, 1985; Ramírez, 1995, 2003; Davila, 2003). Platnick and Lau (1975) compared claw tufts of representatives of Anyphaenidae and Clubionidae, however, without discussing the fine structure of setae and their adhesive function. Ubick and Vetter (2005) demonstrated differences in the origin of claw tufts in Dionycha and three-clawed spiders. Spatular dimensions and densities were previously compared in eight spider species (Peattie and Full, 2007) without a detailed description of the spider attachment system and its relationship to the biology of the species studied.

The present paper is a comparative scanning electron microscopy study of scopulae in sixteen wandering spider species from different families. Morphological features are discussed according to their possible functional significance. The following questions were asked. (1) Is there any correlation between different micromorphological variables in the species studied? (2) Are there any trends in the spatial distribution of different adhesive setae and their spatulae? (3) Does scopula structure correlate with the species' habitat? (4) Are there similar evolutionary trends present in different groups of spiders?

2. Material and methods

Scopulae of sixteen araneomorph species from eleven families were studied: *Agroeca brunnea* Blackwall 1833 and *Agroeca cuprea* Menge 1873 (Liocranidae), *Anyphaena accentuata* Walckenaer 1802 (Anyphaenidae), *Clubiona caerulescens* Koch 1867 (Clubionidae), *Cupiennius salei* Keyserling 1877 (Ctenidae), *Drassyllus praeficus* Koch 1866 (Gnaphosidae), *Ebrechtella tricuspidata* Fabricius 1775 (Thomisidae), *Evarcha arcuata* Clerck 1757 (Salticidae), *Heliophanus cupreus* Walckenaer 1802 (Salticidae), *Micrommata virescens* Clerck 1757 (Sparassidae), *Oxyopes heterophthalmus* Latreille 1804 (Oxyopidae), *Philodromus cespitum* Walckenaer 1802(Philodromidae), *Thanatus formicinus* Clerck 1757 (Philodromidae), *Tibellus oblongus* Walckenaer 1802 (Philodromidae), *Zelotes subterraneus* Koch 1833 (Gnaphosidae) and *Zora spinimana* Sundevall 1833. Specimens were collected in the Ukraine, with the exception of *C. salei*, which comes from a laboratory stock (Department of Neurobiology of the University of Vienna, Austria). The specimens were fixed and stored in 70% ethanol. Mainly single female specimens were analysed, except in *E. arcuata*, *H. cupreus*, *O. heterophthalmus* and, *T. oblongus*, where both sexes were analysed. The four walking legs on one side of the body were cut off, dehydrated in an ascending series of ethanol, critical point dried and sputter-coated with a 15 nm thick layer of gold–palladium. Specimens were observed at 20 kV in a Hitachi S-800 scanning electron microscope (SEM). Micrographs at magnifications of 80–800 were used for an overview, magnifications of 2000–4000 for analysis of the setae, and magnifications of 10,000–20,000 for analysis of setules. For measurements of structures from SEM-micrographs, DatInf® Measure software (DatInf GmbH, Tübingen) was used. The following parameters were quantified: length, width and total area of the claw tuft, number and density of setae, setal width at the tip, at the distal, and proximal parts of the claw tuft. Additionally, both the setule density and spatula width in the distal and proximal parts of the claw tuft were measured. Furthermore, the presence of tarsal and metatarsal scopulae was analyzed.

3. Results

3.1. Scopula morphology

Clubiona caerulescens Koch 1867 (Clubionidae)

C. caerulescens is a nocturnal wandering spider of medial size (♀ 6–10 mm, ♂ 6–8 mm) that is wide-spread throughout Europe. It lives in woods on deciduous trees and shrubs, where it searches actively for prey and captures it using the anterior legs. *Clubiona* sp. can easily walk on smooth surfaces like glass (personal observation).

Claw tufts are of an oval shape being one third longer than wide. L1 and L2 (anterior legs) have a claw tuft of similar dimensions with about 90 setae and an area of about 11×10^3 μm^2 (Fig. 2B). Claw tufts on L3 and L4 (posterior legs) are three times larger and consist of 205 (L3) and 225 (L4) setae, respectively. L4 bears the biggest claw tuft (Fig. 2C) with an area of 31×10^3 μm^2 and double the length (300 μm) and width (170 μm) in the anterior legs. Setal density is high in L1 (8.3×10^{-3} μm^{-2}) and lower in the other legs (about 7.5×10^{-3} μm^{-2}). L1 also differs from the others legs (4.1 μm^{-2}) in the setule density (3.4 μm^{-2} in setae of the proximal part of the claw tuft). Claw tuft setae are attached to the underlying cuticle through the socket (Fig. 2D inset), which is shaped in such a way that setal movement is guided by the socket in a predefined (lateral) direction. Setae are S-shaped and their sockets are directed to the claw tuft centre. These features might influence setal spring properties, which were previously assumed to be important in generating adhesion in spiders (Gasparetto et al., 2009). Setae become gradually flattened and broadened at the tip, which ends in a fringed edge (Fig. 2D). The width of the setal tip differentiates increasingly from the proximal to the distal part of the tuft. There are some differences between the anterior and posterior legs. For example, in L1, seta width is, on average, 10.6 μm in the proximal part of the claw tuft and 11.6 μm in the distal part, while 7.9 μm and 15.1 μm, respectively, in L4. The spatula is triangular shaped and slightly curved. Its average width is rather regular in the range of 0.22 μm except in L4, where spatulae bear double widths (0.45 μm).

L1 and L2 have dense scopulae located at the ventro-lateral sides of both the tarsus and metatarsus. Setae in these parts have a rounded shape. Setules coverage appears on the side that is facing the tarsus (Fig. 2E), and might be activated by erection, caused by an increase in hydraulic pressure within the leg, as has been previously described for lycosid and salticid scopulae (Rovner, 1978; Foelix et al., 1984). The direction and the angle of setal movement is determined by the kidney-shaped hair sockets (Fig. 2E inset).

Zora spinimana Sundevall 1833 (Zoridae)

Z. spinimana is the most abundant zorid spider in Europe. It has a body length of 4.5–6.5 mm. It is a ground dwelling, pursuing hunter, which can be found in leaf litter and open sites.

Claw tuft and setal structure are comparable to those of *C. caerulescens*. Relative to the smaller size of *Z. spinimana*, its claw tufts are smaller than those in *C. caerulescens*: with an area of 13×10^3 μm^2 on L3 and 15×10^3 μm^2 on L4 (Fig. 2F), and the posterior legs of *Z. spinimana* have claw tufts two times smaller than those in *C. caerulescens*. The difference between posterior and anterior claw tufts in *Z. spinimana* is less expressed than in the compared species: With an area of 10×10^3 μm^2 on L1, the tuft is only about one third smaller than that of L4. The smallest pretarsal scopula is in L2 (8×10^3 μm^2). Setal density in this species is higher than in clubionids: about 10.0×10^{-3} μm^{-2} on L1 and L2, 9.0×10^{-3} μm^{-2} on L3, and 7.8×10^{-3} μm^{-2} on L4. Each seta ends in a point, but some setae are massively broadened in their distal parts (Fig. 2F inset). Setae in the proximal part of the tuft are less broadened and more tapered.

Average setal width is about 10.6 μm in the distal and 7.5 μm in the proximal parts of the claw tufts in all legs. Setule density is about 2.5 μm^{-2} in distal scopula parts. Spatula width is higher than in *C. caerulescens* and shows a gradient from the anterior (0.62 μm in L1) to posterior part of the scopula (0.48 μm in L4).

The claw tuft is surrounded by long (about 125 μm long) tactile hairs. Tarsal claws are relatively small. The leg scopula is not very