The covering setae of ground spiders (Araneae: Gnaphosidae)

Boris Zakharov & Vladimir Ovtsharenko

doi: 10.5431/aramit4904

Abstract. Previous study of the setae covering the opisthosoma of ground spiders shows that the morphology of the covering setae is genus-specific. The present study pursues the description of covering setae across the whole Gnaphosidae family using SEM. A detailed morphology of the setae of ground spiders (Araneae, Gnaphosidae) is presented. The six major types of covering setae recognized among gnaphosid spiders are squamose, plumose, lanceolate, pinnate, arborate and sicate setae. Squamose setae are characteristic for *Micaria lenzi* and *Nauhea tapa*. Plumose setae are more common in ground spiders and occur in the genera *Drassodes*, *Haplodrassus*, *Anagraphis*, *Nodocion*, *Zelotes* and the species *Berlandina caspica*, *Nomisia aussereri*, *Minosiella intermedia*, *Sosticus loricatus*, *Leptodrassus memorialis*, *Intruda signata*, *Parasyrisca caucasica*, *Scopoides catharius*, *Echemoides tofo*, *Zimiromus medius*, *Encoptarthria echemophthalma*, *Apodrassodes trancas*, *Apopyllus silvestri*, *Hemicloea sundevalli*, *Zelanda erebus*, *Orodrassus assimilis*, *Callilepis nocturna* and *Synaphosus turanicus*. The species *Matua valida*, *Anzacia gemmea*, *Hypodrassodes maoricus*, *Homoeothele micans* and *Scotophaeus blackwalli* have lanceolate setae. Spiders of the genus *Gnaphosa* have pinnate setae. *Fedotovia uzbekistanica* has arborate setae. The species *Cesonia bilineata*, *Herpyllus propinquus*, *Litopyllus temporarius*, *Aphantaulax seminigra* and *Kishidaia conspicua* have sicate setae. Some genera, such as *Drassodes* and *Synaphosus*, have a combination of different types of setae on their opisthosoma, whereas others, like *Eilica* sp., *Laronius erawan*, *Urozelotes rusticus*, have no covering setae on their opisthosoma at all. This study reveals the existence of different types of covering setae and provides a set of characteristics important for the classification and phylogenetic analysis of Gnaphosidae.

Keywords: arborate, lanceolate, pinnate, plumose, sicate, squamose setae

All ground spiders possess setae that cover their bodies. Ovtsharenko (1983, 1985, 1989) and after that Murphy (2007) recognized 10 different types of setae on the cuticle of ground spiders. Setae have different morphologies and diverse functions, depending on their location on the body (Ovtsharenko 1985, 1989). Aculeate setae are the most common type of setae on the cuticle. These setae are widely distributed over the spider's body. The majority of these setae are sensory organs or mechanoreceptors (Murphy 2007). Covering setae are located mostly on the abdomen, dorsally, ventrally and laterally, and may also cover the cephalothorax, legs, pedipalps and spinnerets. Covering setae have no connection with sensory receptor cells, they have no sensory function (Townsend & Felgenhauer 1998a, 1998b, 1999, 2001, Foelix 2011), and are identified by the following characteristics: (a) the covering setae rest in the shallow depression or small elevation of the cuticle, (b) the pedicel is bent at an obtuse angle where it emerges from the socket, (c) the main axis of the setae is parallel to the surface of the spider's body, and (d) the trunk of the setae has appendages.

The covering setae are of special interest. Lehtinen was among the first who noted the importance of these cuticular structures for spider classification (Lehtinen 1967, 1975a, 1975b). Thus, he called the covering setae 'feathery hairs' on the tibia of *Micaria pulicaria* (Lehtinen 1975b). Hill (1979) and Townsend & Felgenhauer (1998a, 1998b, 1999) made a significant contribution to our understanding of the diversity of the shapes of these cuticular structures, which they called 'scales'. Studies of ground spiders (Araneae: Gnaphosidae) demonstrate that they are greatly varied in shape and are genus-specific (Ovtsharenko 1983, 1985, 1989, Murphy 2007). The value of scales for classification and establishing evolutionary relationships were demonstrated for jumping spiders (Hill 1979) and lynx spiders (Townsend & Felgenhauer 2001). The wide diversity of scales and their value for phylogenetic analysis were used for the reconstruction of the phylogeny of araneomorph spiders (Griswold et al. 2005, Ramírez 2014). However, knowledge about the diversity of the covering setae among gnaphosid spiders is far from complete and still has to be addressed. As Murphy (2007: 31) said: "A serious study of spider setae may yet reveal much of interest".

Boris ZAKHAROV, Department of Natural Sciences, La Guardia Community College of the City University of New York, New York, USA, e-mail: bzakharov@lagcc.cuny.edu
Vladimir OVTSHARENKO, Department of Natural Sciences, Hostos Community College of the City University of New York, New York, USA, e-mail: vio@hostos.cuny.edu

submitted 12.11.2014, accepted 21.5.2015, online: 10.6.2015

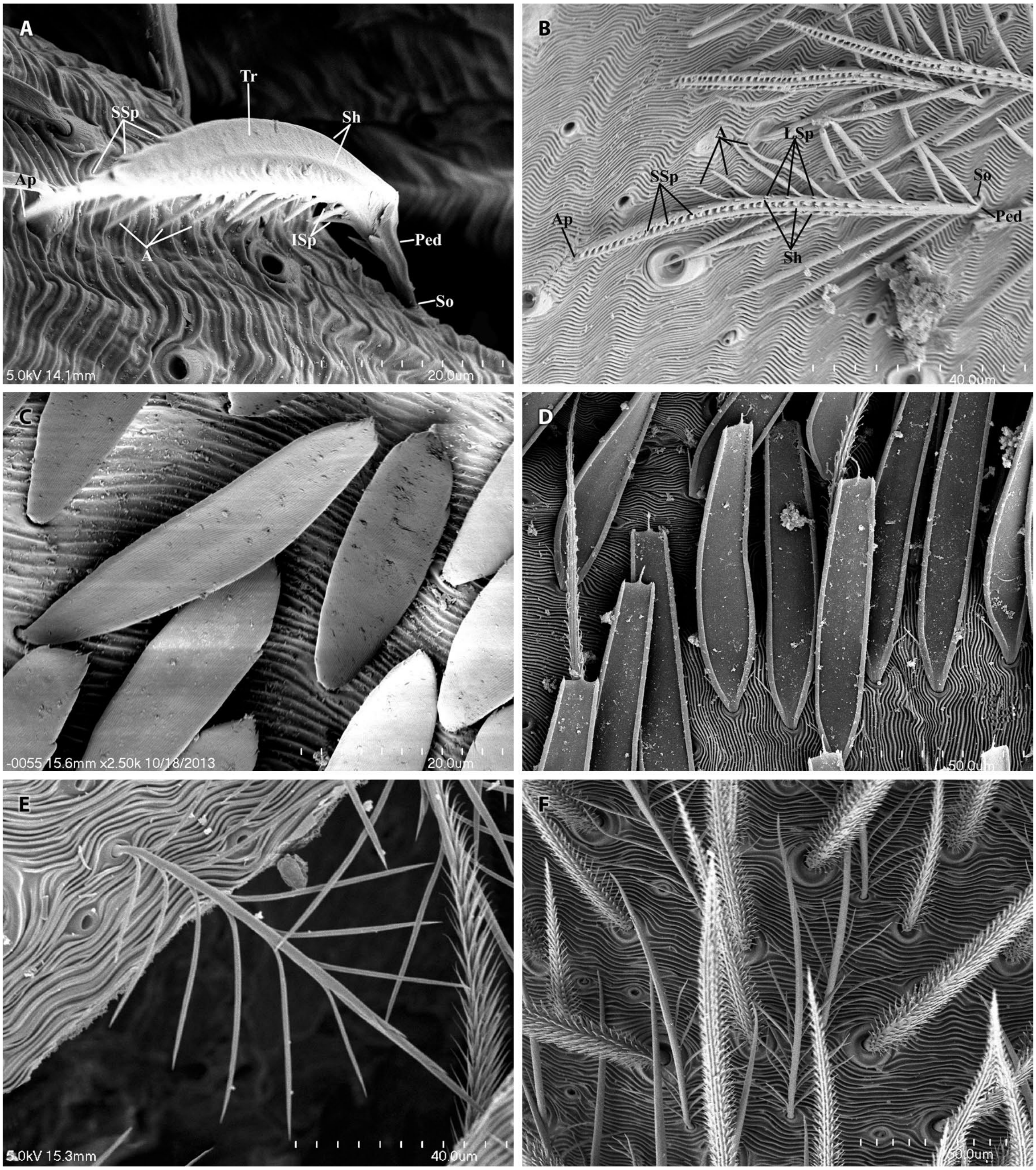

Fig. 1: External features of covering setae; squamose (c and d), sicate (a) and plumose (b, e and f) setae on abdomen of gnaphosid spiders. **A.** *Cesonia bilineata*; **B.** *Anagraphis sp.*; **C.** *Micaria lenzi*; **D.** *Nauhea tapa*; **E.** *Echemoides tofo*; **F.** *Drassodes lapidosus*; A – appendages, Ap – apex, Ped – pedicel, ISp – inferior spines, SSp – superior spines, Sh – shafts, So – socket, Tr – trunk.

In this study, we use the term 'covering setae' based on the following reasoning: 1. A scale is thin, flat plate, which is the most common shape for these structures among jumping and lynx spiders. However, this type of shape is comparatively rare among gnaphosids. Ground spiders often have feather-shaped setae, far from being a flat plate. 2. The term feathery hair was first used by Lehtinen for these structures (Lehtinen 1975b, Fig. 7, image 12). 3. In studies of ground spiders (Araneae: Gnaphosidae) the term 'setae' was traditionally used for these structures (Ovtsharenko 1983, 1985, 1989, Ovtsharenko et al. 1994, 1995, Ovtsharenko & Platnick 1995, Platnick et al. 2001, Murphy 2007). Thus, in the article on spiders of the genus *Synaphosus* the authors wrote that the abdomen of the spider is "covered by thick, plumose setae bearing 4-7 pairs of appendages originating from ventral surface of setae (figs. 5, 6)" (Ovtsharenko et al. 1994, p. 3).

Materials and methods

Specimens were examined with a Hitachi S-4700 Field Emission SEM at the American Museum of Natural History (New York). The cut-off abdomen was dehydrated in acetone, critically point dried in carbon dioxide, mounted with double-sided sticky carbon tape, and sputter coated using the necessary materials. The resulting images were combined using Photoshop.

Setae terminology follows Simon (1893), Berland (1919), Lehtinen (1975a, 1975b), Platnick (1975), Hill (1979), Ovtsharenko (1983, 1985, 1989), Townsend & Felgenhauer (2001) and Murphy (2007). Collections examined: AMNH - American Museum of Natural History, New York, USA; NMNZ - National Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; OMD - Otago Museum, Dunedin, New Zealand; OPC - V. Ovtsharenko personal collection; SAM - South Australian Museum, Adelaide, Australia; ZDUC - Zoological Department of the University of Canterbury, Christchurch, New Zealand; ZISP - Zoological Institute Saint Petersburg, Russia.

The following species were studied (locality and collection included): *Anzacia gemmea* (Dalmas, 1917) [NEW ZEALAND: Kaikoura, January, 1961; OMD]; *Anagraphis* sp. [KAZAKSTAN: Atyrau District, Ustyurt Natural Reserve, Ustyurt Plateau, village Kemderlie, May 20, 1989, coll. I. I. Ibraev and A. A. Zyuzin; OPC]; *Apodrassodes trancas* Platnick & Shadab, 1983 [ARGENTINA: El Bolsón, Rio Negro, September 1962, coll. A. Kovacs; AMNH]; *Apopyllus silvestri* (Simon, 1905) [ARGENTINA: Epuyén, Chubut, June 12, 1962, coll. Andor Kovacs; AMNH]; *Berlandina caspica* Ponomarev, 1979 [AZERBAIJAN: village Dubendy, May 21, 1977, coll. Dunin; OPC]; *Cesonia bilineata* (Hentz, 1847) [USA: Arkansas, Logan Co., mountain Magazine, Mossback Ridge Bluff, July 20, 1990, pitfall trap, coll. B. Leary; AMNH]; *Drassodes lapidosus* (Walckenaer, 1802) [AZERBAIJAN: Pirgulu State Reserve, 1300 m, May 21, 1984, coll. D. Logunov; OPC]; *Echemoides tofo* Platnick & Shadab, 1979 [CHILE: Coquimbo, Llano de la Higuera, September 29, 1980, coll. L. E. Péna; AMNH]; *Encoptarthria echemophthalma* (Simon, 1908) [AUSTRALIA: Belair Natural Park, 300 m S Lower Waterfall, 35⁰01'S, 138⁰43'E, pitfall, November 28-December 5, 1994, coll. E. G. Matthews, J. A. Forrest; SAM]; *Fedotovia uzbekistanica* Charitonov, 1946 [KAZAKHSTAN, Muyunkum District, 51 km of highway Mirnyi-Khantau, June 8-9, 1990, coll. A. A. Fedorov; ZISP]; *Gnaphosa muscorum* (L. Koch, 1866) [RUSSIA: Chita Region, Sokhondo Natural Reserve, river Upper Bukukun, pitfall trap, July 21, 1990, coll. S. Danilov; OPC]; *Gnaphosa taurica* Thorell, 1875 [KIRGHIZSTAN, Kirghiz-Ata gorge, northern slope, June 11, 1985, coll. A. A. Zuzin, OPC]; *Haplodrassus dalmatensis* (L. Koch, 1866) [AZERBAIJAN: Kashkachay vill., elev. 1000 m, June 24, 1977, coll. Dunin; OPC]; *Haplodrassus soerenseni* (Strand, 1900) [RUSSIA: Altai, Turochak District, Altai Mountains, pine forest, pitfall trap, coll. S. B. Ivanov; OPC]; *Homoeothele micans* Simon, 1908 [AUSTRALIA: 3.1 km WNW Mount Lindsay, 27⁰01'09"S, 129⁰51'01"E, Pitjantjatjara lands Survey WAT 03, pitfall trap, October 1996; SAM, N 9061-2]; *Hypodrassodes maoricus* Dalmas, 1917 [NEW ZEALAND: Wellington, Karori, inside house, November 8, 1995, coll. C. Palma; NMNZ]; *Intruda signata* (Hogg, 1900) [NEW ZEALAND: Auckland, Beechlands, 36°53'S, 174°46'E, Jan. 1951, coll. J. Campbell; OMD]; *Leptodrassus memorialis* Spassky, 1940 [RUSSIA: Rostov Region, Zavetninskye district, 4 km S.-E. vil. Fedoseevka, clay riverbank, June 15, 1973, coll. Ponomarev; OPC]; *Leptodrassus* sp. [KAZAKHSTAN: Atyrau, Ustyurt Natural Reserve, Usturt Plateau, Baskorgan wells, May 28, 1989, coll. A.A. Raikhapov, S. I. Ibraev; OPC]; *Litopyllus temporarius* Chamberlin, 1922 [USA: Black Rock Forest, Cornwall, NY, 41.42267°N, 74.03039°W, July 5, 2009, coll. V. Ovtsharenko, B. Zakharov; OPC]; *Matua valida* Forster, 1979 [NEW ZEALAND: Arrowtown, December 3, 1969, under stone, coll. R. R. Forster; OMD]; *Micaria lenzi* Bösenberg, 1899 [RUSSIA: Magadan Region, Tenkinskye district, Sibit-Tiellakh village, May 15, 1983, coll. S. Buhkalo; OPC]; *Minosiella intermedia* Denis, 1958 [TURKMENISTAN: Repetek, April 6, 1981, coll. V. A. Krivohatsky; OPC]; *Nauhea tapa* Forster, 1979 [NEW ZEALAND: Logan Burn,

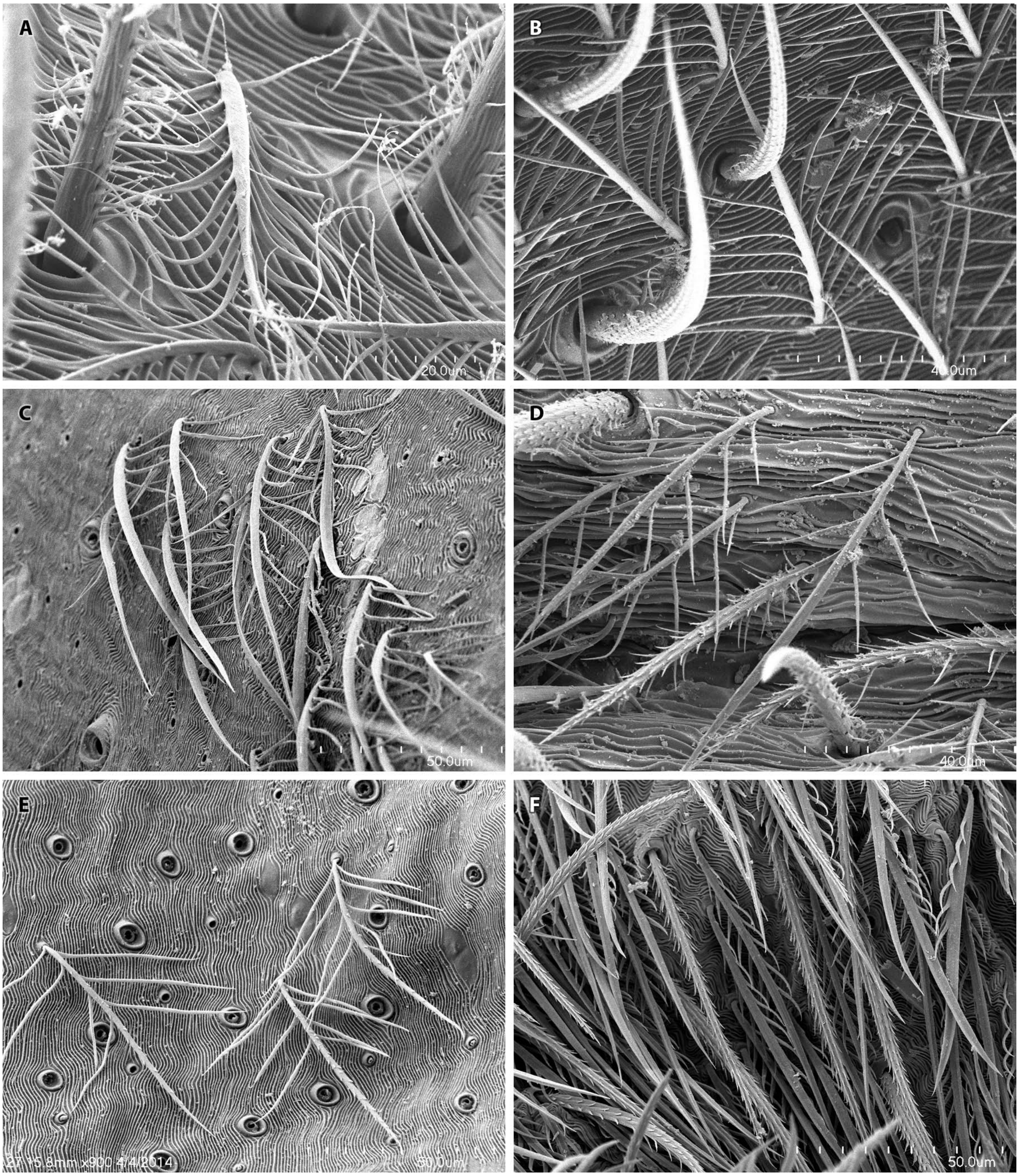

Fig. 2: Plumose setae on the abdomen. **A.** *Berlandina caspica*, **B.** *Nomisia aussereri*, **C.** *Haplodrassus dalmatensis*, **D.** *Sosticus loricatus*, **E.** *Leptodrassus memorialis*, **F.** *Synaphosus turanicus*.

11-23 February, 1983, 900 m, pitfall trap, coll. B. I. P. Barratt; OMD]; *Nodocion eclecticus* Chamberlin, 1924 [USA: Tucson, Arizona, coll. O. Bryant; AMNH]; *Nodocion mateonus* Chamberlin, 1922 [USA: Lake Co.: Albert Lake, July 2, 1961, coll. B. Malkin; AMNH]; *Nomisia aussereri* (L. Koch, 1872) [AZERBAIJAN: Kuba, Tenshalti, September 26, 1984, coll. unknown; OPC]; *Orodrassus assimilis* (Banks,

1895) [USA: Oregon, Willow Creek Camp, Warner Mountains, Lake Co., June 22, 1952, coll. B. Malkin; AMNH]; *Parasyrisca caucasica* Ovtsharenko, Platnick & Marusik, 1995 [RUSSIA: Caucasus, Krasnodar Region, Caucasian Reservation, Mountain Mramornaia, 2500 m, July 27, 1975, coll. V. I. Ovtsharenko; OPC]; *Pterotricha* sp. [UZBEKISTAN: Bukhara region, 70 kn W of Utch-Kuduk, 30 km SW of the village Minbulak, sand desert, coll. D. V. Logunov; OPC]; *Pterotricha strandi* Spassky, 1936 [TURKMENISTAN: Repetek, June 14, 1979, coll. V. A. Krivokhatsky; OPC]; *Scopoides catharius* (Chamberlin, 1922) [USA: California, 1-2 mi W of Lane Pine, Inyo Co., April 27, 1960, coll. W. J. Gertsch, Ivie and Schrammel; AMNH]; *Scotophaeus blackwalli* (Thorell, 1871) [USA: California, Glendale, October 15, 1951, coll. Ted Tice; AMNH]; *Sosticus loricatus* (L. Koch, 1866) [UZBEKISTAN: Tashkent district, village Toitepa, June 18-30, 1981, coll. N. M. Kudrina; OPC]; *Synaphosus turanicus* Ovtsharenko, Levy & Platnick, 1994 [KAZAKHSTAN, Atyrau, District, Ustyurt Natural Reserve, Ustyurt Plateau, Baskorgan wells, May 25, 1989, coll. A. A. Raikhapov, S. Ibraev, V. Ovtsharenko; OPC]; *Zelanda erebus* Foster, 1979 [NEW ZEALAND: Gainesville; ZDUC]; *Zelotes lasalanus* Chamberlin, 1928 [USA: Arizona, Tucson, coll. O. Bryant; AMNH]; *Zimiromus medius* (Keyserling, 1891) [BRAZIL: S. Paulo, S. Bocaina, 1960 m, S. Jose Barreiro, November 1968, coll. M. Alvarenga; AMNH].

Results

Almost all ground spiders (Araneae: Gnaphosidae) have covering setae. Some species possess a combination of different types of setae on their body. Density of the setae varies on the spider's body. Some species have few setae loosely scattered over the dorsal side of the abdomen. In other species, setae entirely cover the opisthosoma, cephalothorax and legs, and create the shingle-like overlapping coverage that may be iridescent as in *Nauhea tapa* (Fig. 1D). The covering setae rest in a shallow depression of the cuticle that is slightly elevated above the integument surface or located on small tubercle of the cuticle. The pedicel of the seta is bent at an obtuse angle after it emerges from the socket on the cuticle. As a result of this bending, the main axis of the setae is parallel to the surface of the spider's body (Fig. 1A, B).

Setae have a comparatively short pedicel bent on one side, and an apex – on the other side. The apex may be sharp, flattened, or rounded (Fig. 1C, D). In *Gnaphosa* the apex bifurcates (Fig. 6E). The trunk of the setae consists of fused shafts. Often there are three shafts that create ridges of the trunk (Fig. 1A, B). Following Hill (1979), short triangular outgrowths are defined as spines. There are superior spines (SSp) that are located on the upper surface of the trunk, lateral spines (LSp) on both sides, and inferior spines (ISp) on the side of the trunk that faces the body surface (Fig. 1A, B). The inferior spines often have a hook-like shape and, probably, provide a connection between the seta and the body surface (Murphy 2007). Setae may also have long outgrowths called appendages (A) (Fig. 1A, B). Depending on the shape of the setae shaft and types of accessory structures, there are six major types of covering setae among gnaphosid spiders: squamose, plumose, lanceolate, pinnate, arborate and sicate.

Squamose setae are flat and broad. They are comparatively short. They may bear some accessory structures and may have a spinous apex. Usually, this type of seta creates a dense, iridescent coverage of the spider's abdomen and cephalothorax (Fig. 1C, D). Squamose setae are characteristic of small ground spiders: *Micaria* and *Nauhea*. Thanks to the iridescent squamose setae these spiders have a metallic blue to green colour. *Micaria* demonstrates the diversity of squamose setae, which take many forms and may or may not have proximal appendages. The sides and tips of the setae are serrated. Murphy called this type "uncinate squamose setae". These setae show variation in size and shape. The side of some setae which face towards the body bears hook-like inferior spines (Murphy 2007). The tip of the setae may be serrated or have a sharp spike (Fig. 1C). Murphy thought that "uncinate squamose setae" are a characteristic feature of *Micaria* (Murphy 2007). In the New Zealand spider *Nauhea tapa* the pedicel of the seta proximally bears one or two pairs of appendages. The tip of the setae is wide, serrated, and with a sharp terminal spike (Fig. 1D).

Plumose setae are bilateral and look like a feather. Lehtinen (1967) called this type of seta a "feathery hair". Later he came to the conclusion that all types of feathery setae are adaptations of a setal structure that has appeared many times independently and may be regarded as different modifications of the plumose seta type (Lehtinen 1975b, see Fig. 7.12). Thus, we adopt the term "plumose setae" as the basic name for all variations of this type of setae. These

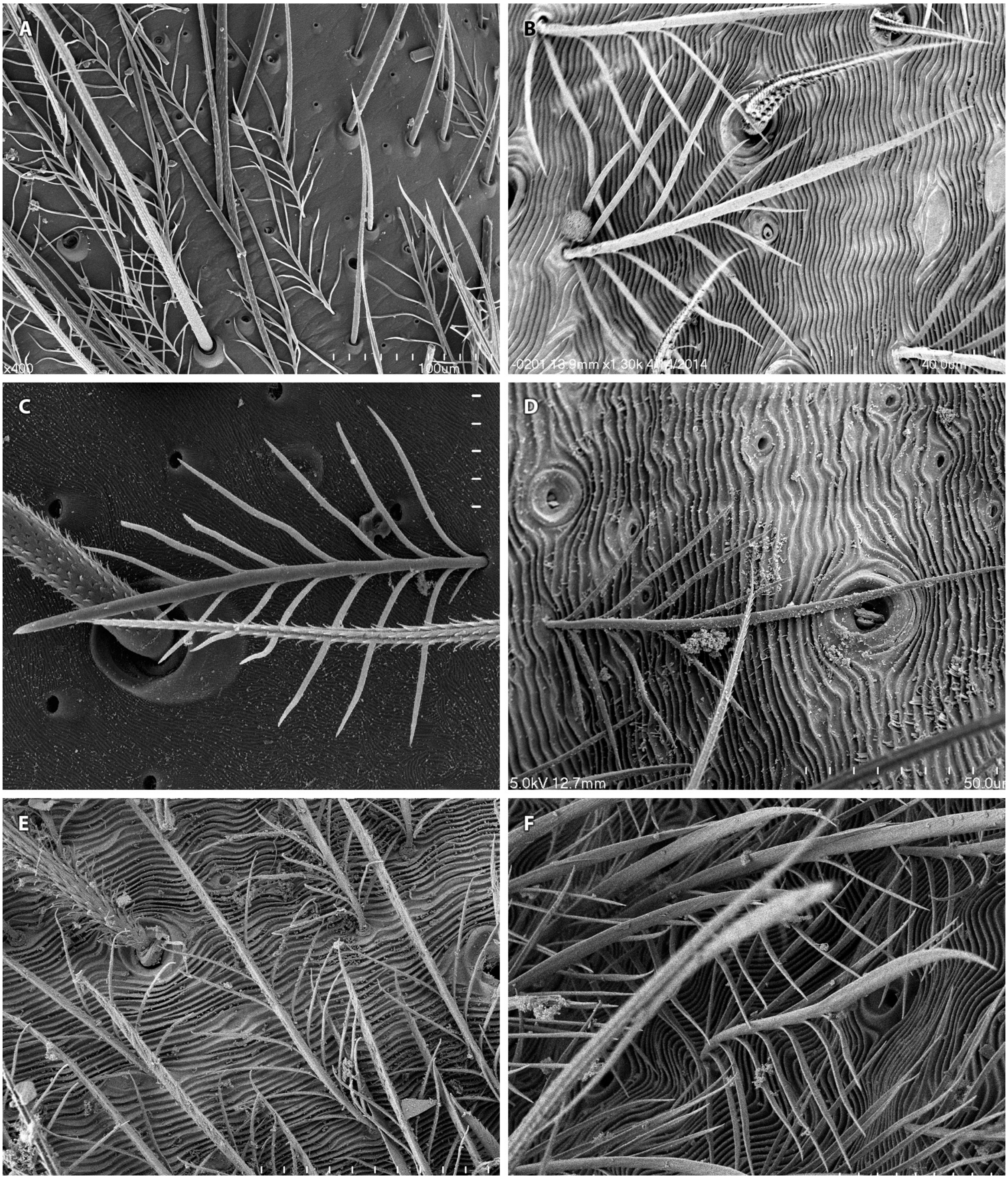

Fig. 3: Plumose setae on the abdomen (B, D, E, F), cephalothorax (C), and legs (A). **A.** *Intruda signata*, **B.** *Zimiromus medius*, **C.** *Encoptarthria echemophthalma*, **D.** *Apodrassodes trancas*, **E.** *Apopyllus silvestri*, **F.** *Minosiella intermedia*.

setae have a long narrow trunk, sharp at the apex. The comparatively long appendages are branched from both sides of the trunk. The appendages may be set along the whole length of the trunk, or only on a part of it, usually the proximal third of the trunk length. The position and length of appendages are also greatly varied and may provide significant features for the spiders' classification (Figs 2, 3, 4). The middle part of the trunk is enlarged, whereas its tip is sharpened. Appendages are set in two rows on the lateral sides of the trunk. The total number of appendages is genus-specific and varies from 2 to 44. The appendages may be long, slender, and sharp at the tip, or enlarged in their middle part, or clavate, i.e. enlarged at the tip. As a rule, appendages are more or less of the same length. However, there are exceptions. In these cases, the longest appendages are situated at the base of the trunk, and the shortest ones closer to its tip. The setae are immovably attached to the body surface on the cuticular elevation that has fine longitudinal stripes. The trunk of the setae bends proximally. This position and their immovable attachment are characteristic for covering setae only. All other setae are at a right angle or significantly far away from the integument. This suggests that plumose setae are mostly covering structures, have a protective function for the spiders' integumentary system, and do not have a sensory function (Foelix 2011). They are always present on the dorsal side of opisthosoma. They may create a continuous coverage or may be loosely distributed over the body surface (Ovtsharenko 1985).

The plumose setae of *Berlandina*, *Nomisia*, *Minosiella* and *Pterotricha* have lateral appendages along almost their entire length. The upper part of the setae that have no appendages may be only $^1/_4$-$^1/_5$ of its length as in *Nomisia* (Fig. 2B), *Minosiella* (Fig. 3F) and *Pterotricha* (Fig. 4D), or even less, as in *Berlandina* (Fig. 2A) (Ovtsharenko 1985). The number of appendages is also different. *Minosiella intermedia* has 11-18 appendages, *Pterotricha strandi* – 23-38. In *Nomisia*, it is 10-20, whereas in *Berlandina* it is 30-44 appendages or 15-22 pairs. The structure of the setae may change, depending on the body part. The abdominal setae of *Berlandina*, for example, have 30-32 appendages; setae on the carapace may have up to 44 appendages. *Nomisia* has setae with 10-12 pairs of appendages on its abdomen, 10-16 pairs on its carapace, and 10-20 pairs on the legs. In all these genera, the plumose setae create a dense coverage that completely covers all of the spider's body (Ovtsharenko 1985).

Species of the genera *Haplodrassus* (Fig. 2C) and *Drassodes* (Fig. 1F) have at the tip a clear part of their plumose setae two times longer than its base, which bears lateral appendages. The number of appendages varies. *Haplodrassus dalmatensis* has 8-14 appendages (Fig. 2C), *Haplodrassus soerenseni* has 8 appendages. *Haplodrassus signifier* has from 7 to 10 appendages (Ovtsharenko 1985, 1989). The number of appendages in this species is different on both sides of the setae's trunk. Setae on one side may have one or even three fewer appendages than on the other side. Often, if on one side it is even, then on the other it is uneven (Ovtsharenko 1985). The plumose setae of *Drassodes* vary in number from 8 to 14, but the most common is 10 (Fig. 1F).

In *Sosticus* (Fig. 2D) and *Leptodrassus* (Fig. 2E) the tip part is equal or only a little longer than the base with its appendages attached. *Sosticus* has 8-14 appendages. These appendages are of different lengths. The longest appendages are in the middle part of the trunk. *Leptodrassus memorialis* has 8-11 appendages. The tip of the setae is laterally serrated. *Intruda signata* has plumose setae with 9 appendages at the base of the trunk; 4 appendages on one side and 5 appendages on the other side (Fig. 3A).

Plumose setae of *Anagraphis* have 12-15 appendages. The appendages are not organized into pairs. Their number on opposite sides of the trunk is different. Usually, if on one side there are six appendages, the other side has eight. Beside that the setae of *Anagraphis* spiders have two rows of superior spines (SSp) and lateral spines (LSp) along the total length of the trunk (Fig. 1B). Plumose setae on the abdomen of *Nodocion meteonus* possess 12 long appendages, occupying almost half of the trunk, and 5-6 long spines distributed on the distal part of the setae; all trunk and appendage setae have fine, longitudinal ridges (Fig. 4A). In *Parasyrisca caucasica* on the abdomen there are plumose setae with 13 appendages; all appendages have different lengths (Fig. 4C). Plumose setae on the abdomen of *Scopoides catharius* have 5-15 appendages, they occupy less than half of the proximal part of the trunk; the distal part of the trunk is coved by short spines and look like scales (Fig. 4F). Plumose setae of *Echemoides tofo* have 9-11 appendages. Their number on both sides may be different and vary from 4 to 6. All of these appendages are located at the proximal $^1/_3$ of the trunk. The SSp are distributed along the total length of the trunk from the pedicel to the apex (Fig. 1E). *Zimiromus medius* has plumose setae with 10 appendages. Appendages are long and are flattened in a dorso-ventral direction. The apex of the trunk is sharp. Superior and lateral spines are also present (Fig. 3B). *Encoptarthria echemophthalma* has plumose setae with 7-8 pairs of proximal appendages, the distal part of the trunk is short, less than $^1/_3$ of the trunk (Fig. 3C). *Apodrassodes*

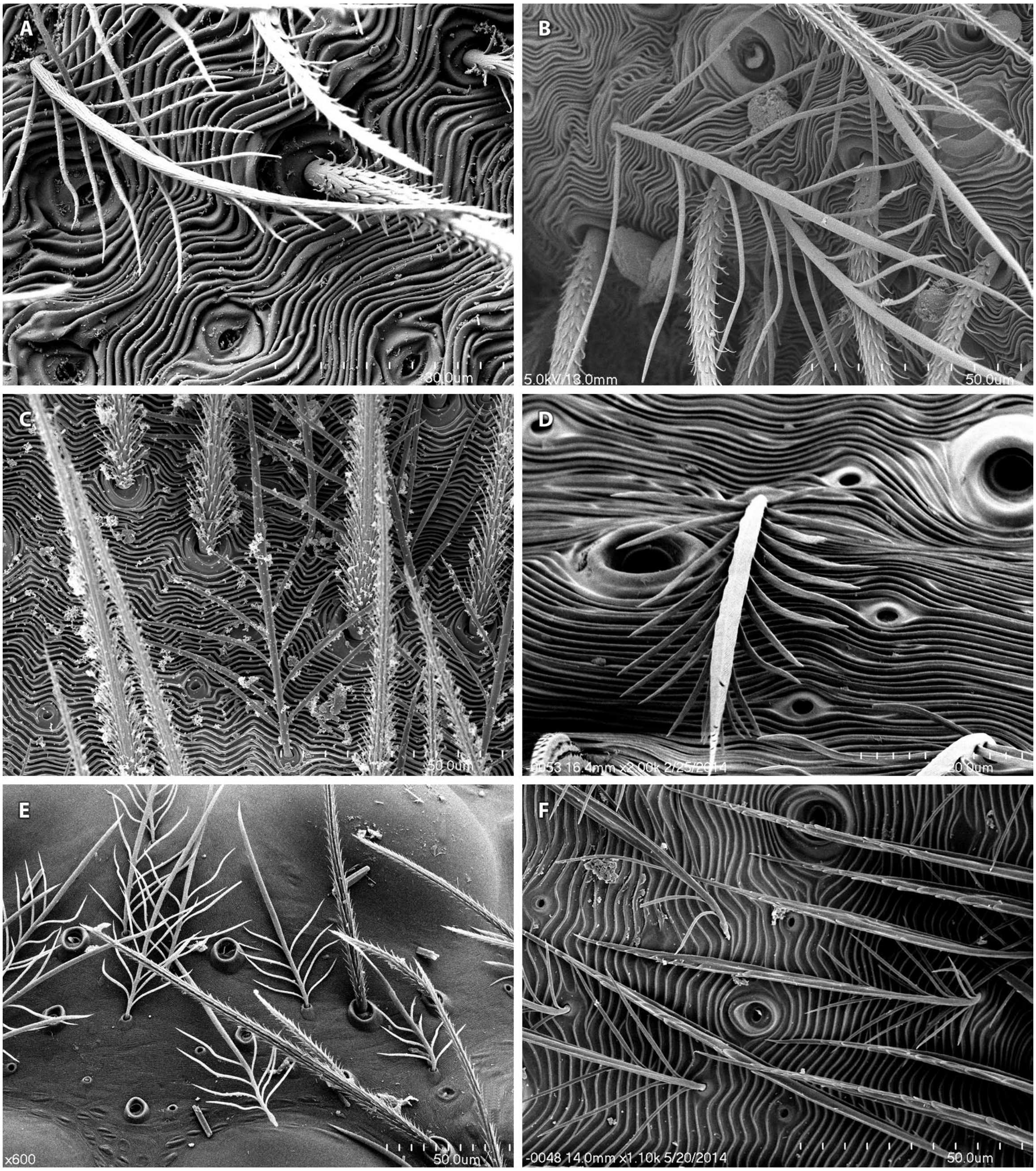

Fig. 4: Plumose setae on the abdomen (A, B, C, D, F) and cephalothorax (E). **A.** *Nodocion meteonus*, **B.** *Orodrassus assimilis*. **C.** *Parasyrisca caucasica*, **D.** *Pterotricha strandi*, **E.** *Zelanda erebus*, **F.** *Scopoides catharius*.

trancas has plumose setae with 4 pairs (total amount of appendages 8) of appendages symmetrically set on the proximal $^{1}/_{3}$ of the trunk (Fig. 3D). *Apopyllus silvestri* has plumose setae with 6-8 appendages on the proximal $^{1}/_{3}$ of the trunk. The distal $^{2}/_{3}$ of the trunk is flattened (Fig. 3E). *Hemicloea sundevalli* has plumose setae with 4-5 proximal appendages on the base of the trunk. In *Zelanda* there are 4 pairs of proximally situated appendages (Fig. 4E). In *Orodrassus assimilis* the plumose setae possess 4 pairs of appendages, the trunk of the setae is smooth, serrated apically (Fig. 4B). Some genera have a reduced number of covering setae. These spiders may have covering setae only on the abdomen and the legs, most commonly on their femur. As a rule, the number of appendages on these setae varies from 0 to 6. In the case that appendages are absent the trunk remains present on the cuticle. Thus, the plumose setae of the Palaearctic species *Callilepis nocturna* have 4-6 appendages of different lengths on their base (Ovtsharenko 1985). Its North American relative *Callilepis pluto* has 5-8 appendages (Platnick 1975). Species of two genera close to *Callilepis, Eilica* sp. and *Laronius erawan*, completely lost the covering setae. *Synaphosus* (Fig. 2F) has plumose setae with 6-7 pairs of appendages. The tip of the setae is slightly enlarged. It is two times longer than it is wide at its base. For species of the genus *Zelotes* the number of appendages is characteristically decreased. Thus, *Zelotes subterraneus* has 2-4 appendages on its setae, *Z. longipes* has 2-3. The plumose setae in these spiders are only on the dorsal side of the opisthosoma (Ovtsharenko 1985). The setae of *Drassyllus praeficus* do not have appendages at all. The opisthosoma of *Urozelotes rusticus* has no covering setae, only sensillae.

Spiders of the genera *Matua*, *Anzacia, Homoeothele*, *Hypodrassodes* and *Scotophaeus* have lanceolate setae (Fig. 5). The lanceolate setae are, as a rule, flat. An oval ridge ornaments them on both lateral sides. The trunk is slightly bent. The tips of the setae are serrated. This type of setae was found on the dorsal side of the opisthosoma, cephalothorax and legs; setae can be modified depending on their location on the body. The trunk of the setae of *Anzacia gemmea* is comparatively narrow and short, and also bears 4 long appendages in its proximal part, close to the base of the setae. The remainder of the trunk is broad and serrated with a sharp spike on the tip (Fig. 5C) (Ovtsharenko & Platnick 1995). Lanceolate setae on the opisthosoma of *Hypodrassodes maoricus* have one pair of proximal appendages and strongly serrated distal parts of the setae (Fig. 5D). Lanceolate setae on the cephalothorax of *Homoeothele micans* have 4 pairs of appendages in the proximal part that reach the middle of the seta; the distal part of the seta is flat and laterally serrated (Fig. 5E). The lanceolate setae on the abdomen of *Scotophaeus blackwalli* are narrow, smooth, with 3 pairs of long proximal appendages and with 4-5 slender spines at the apical part of the trunk (Fig. 6D). Modification of lanceolate setae occurs in *Matua valida,* thus setae on the abdomen are flat, wide, proximally with 3 pairs of appendages and distally on the tip with 3-4 spines on each side of the seta (Fig. 5A). The lanceolate setae on the legs of *Matua valida* are narrow, flat, with 7-8 long appendages in the proximal part of the seta and slightly serrated distal part of seta (Fig. 5B). Lanceolate setae occur sometimes together with plumose setae, mostly on the abdomen, for example in species of *Drassodes* and *Synaphosus.*

Sicate setae have a broad curved trunk and the appendages are all on one pro-curved side of the trunk, which differentiates them from the lanceolate setae (Fig. 6A-D). These setae were found mostly on the dorsal side of the abdomen and carapace (Ovtsharenko 1985). The species of the genus *Herpyllus* have sicate setae with 10 appendages of equal length set in the middle part of the setae. On its tip there are 1-2 short spines. In *Herpyllus propinquus* sicate setae bear only two rows of short (almost spine-like) 6-8 appendages on the dorsal surface of the distal part of the trunk (Fig. 6B). Beside sicate setae, spiders of this species have plumose setae on the dorsal side of their abdomen. In *Aphantaulax seminigra* and *Kishidaia conspicua* the sicate setae have up to 25-30 appendages, distributed over the whole length of the trunk (Ovtsharenko 1989). In *Cesonia bilineata* sicate setae have 4-36 appendages located on the rim of the trunk along the whole of its length. The tip of these setae bears 8-9 spines dorsally (Fig. 1A, 6A). In *Litopyllus temporarius* 15 short appendages are distributed along the total length of the trunk in two closely spaced rows, and 4 pairs of long appendages are located on the proximal part of the trunk (Fig. 6C).

Pinnate setae are characteristic of the spider genus *Gnaphosa*. They are bilateral and folded along the grooved longitudinal midline. The most peculiar characteristic of this type of setae is a marginal serration, created by short appendages, broad at the base, along the whole length of the trunk. The apex of the setae of *Gnaphosa taurica* bifurcates and has the shape of a snake's tongue (Fig. 6E). The setae of *Gnaphosa lugubris* like *G. taurica* have a longitudinal groove along the whole length of the trunk with lateral boarders bent toward the outside. These boarders have two rows of spines, broad at the base and sharp apically. The pedicel of the setae is narrow and is merged into the depression on the cuticle. Thus, the major characteristics of the setae of these spiders are the four rows of appendages, the grooved shape of the trunk, and the way it merges into the cuticle pedicel. Spiders of this genus have setae only on the

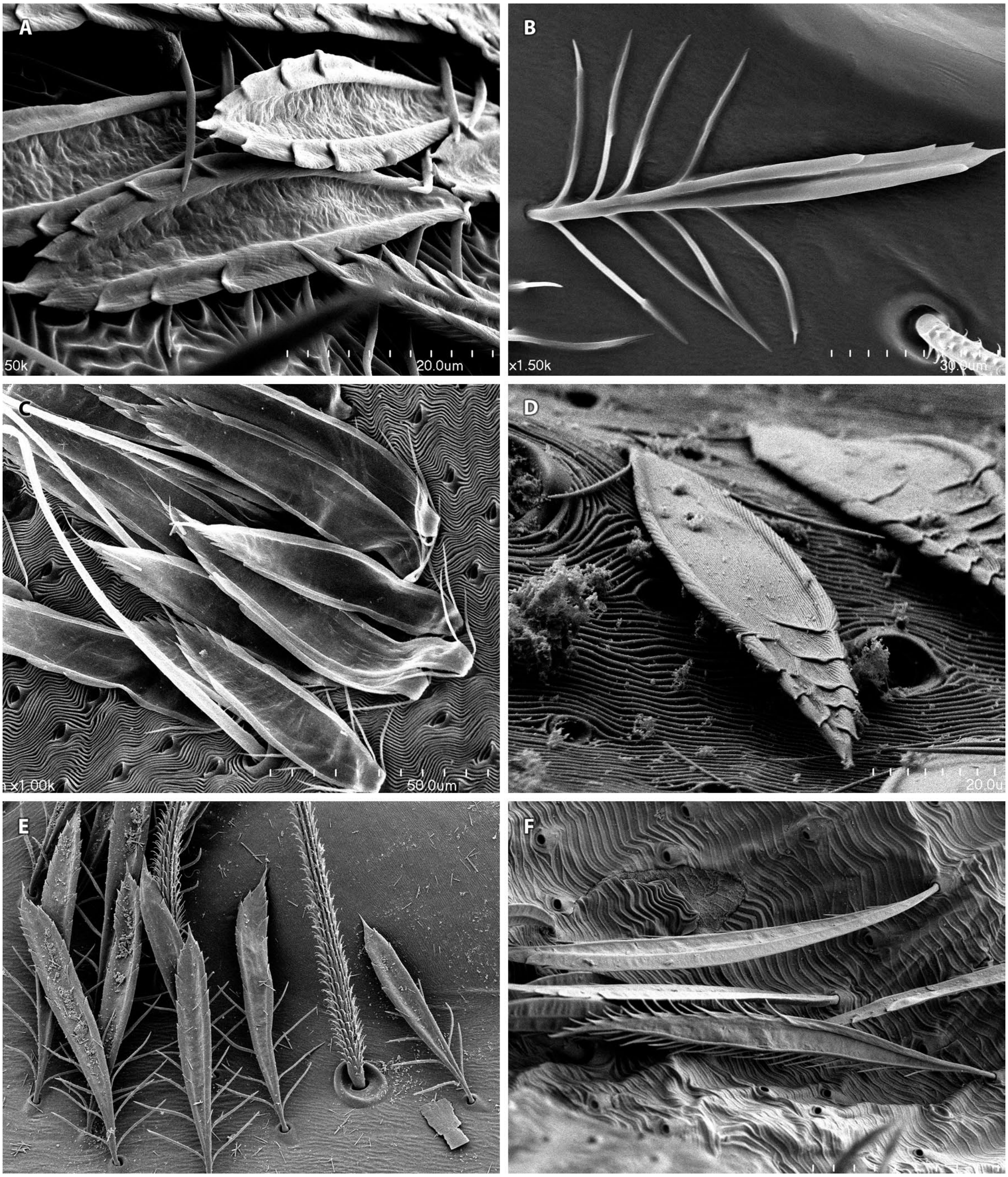

Fig. 5: Lanceolate setae on the abdomen (A, C, D), cephalothorax (E) and legs (B); sicate setae on the abdomen (F). **A, B.** *Matua valida*, **C.** *Anzacia gemmea*, **D.** *Hypodrassodes maoricus*, **E.** *Homoeothele micans*, **F.** *Cesonia bilineata*.

dorsal side of the abdomen, where they create a dense coverage. Comparison of the nymphs of *Gnaphosa lugubris* with adult spiders shows that their setae are almost identical (Ovtsharenko 1985).

Arborate setae occur in the species *Fedotovia uzbekistanica* and this type of setae is the most unusual covering seta among the ground spiders. They look like branches on the trunk of a tree. The trunk of these setae has a shaft with four longitudinal ridges. The appendages are branched from these ridges in four directions almost along the whole length of the trunk (Fig. 6F).

Discussion and conclusions

More than a third of the total known genera of gnaphosid spiders have been studied. The obtained data allow us to make some generalizations. Almost all gnaphosid spiders have covering setae on the dorsal side of their opisthosoma and additionally on the cephalothorax, legs and spinnerets. Some groups of ground spiders have very little (subfamily Zelotinae) or have no covering setae on their abdomen at all (subfamily Laroniinae). Setae demonstrate diverse appearance depending on their location on the body. Our data show the existence of stable characteristics relating to setal morphology. Depending on the shape of the setae and their accessory structures, they may be classified into six groups: squamose, plumose, lanceolate, sicate, pinnate and arborate.

Lehtinen (1967, 1975a, 1975b) was the first who pointed out the value of setal morphology for taxonomy and reconstruction of phylogenetic relationships among spiders. Galiano (1975) and Hill (1979) considered the diagnostic value of salticid scales. Ovtsharenko (1983, 1985, 1989) came to the conclusion that morphology of gnaphosids' covering setae varies among the genera and provides additional characteristics for taxonomic analysis and reconstruction of phylogenetic relationships among ground spiders. Townsend & Felgenhauer (1998a, 1998b, 1999) studied these cuticular structures and showed their usefulness for the taxonomy of oxyopid spiders. Townsend & Felgenhauer (2001), Griswold et al. (2005) and Ramírez (2014) show the importance of these characters in the phylogenetic analysis of Oxyopidae, entelegyne, and dionychan spiders. Our study supports previous observations made by Ovtsharenko (1983, 1985, 1989) that setae in the family Gnaphosidae demonstrate specific subfamilial and generic characteristics and provide valuable information for taxonomy and phylogeny of these spiders.

The role of covering setae still remains unknown. However, the type of seta attachment, the shape of the setae, and the absence of a proven association of the setae with sensory neurons (Townsend & Felgenhauer 1998a, 1998b, 1999, 2001, Foelix 2011) allow us to suggest a protective function. Hill (1979) noted that there are no verified experimental data that may suggest a specific function of the spiders' scales. At the same time, the scales' shape and design create a reflective surface that refracts light and is responsible for the colourful body pattern of jumping spiders that may be displayed during courtship (Hill 1979). Some gnaphosid spiders, such as *Micaria* and *Nauhea*, also have a metallic coloured body created by dense coverage of squamose setae.

Acknowledgments

The present study was supported in part by the Research Foundation of the City University of New York providing funds through the grant PSC-CUNY TRADA-43-582 and the American Museum of Natural History, New York. The authors are grateful to the students Amanda Tsang and Kseniia Rusinova. We are grateful to Henry Towbin and Morgan Hill from the American Museum of Natural History Microscopy and Imaging Facility for technical support with the SEM, as well as Dr. Norman I. Platnick, Curator of AMNH, for support of the study. We are very grateful to Martin Ramírez from the Museo Argentino de Ciencias Naturales, who generously provided us with his beautiful photo of the setae of *Gnaphosa taurica*. The authors are very grateful to Dr. Sandra Dickinson from the LaGuardia Community College of the City University of New York for her valuable help on the text preparation and Don N. Cameron for his help with the proper naming of setae. The authors are indebted to Dr. Martin Ramírez, Hay Wijnhoven and Theo Blick who reviewed this article and gave generously their time and expertise.

References

Berland L 1919 Note sur le peigne métatarsal que possèdent certaines araignées de la famille des Drassidae. – Bulletin du Muséum National d'Histoire Naturelle de Paris, Zoologique 1919: 458-463

Foelix RF 2011 Biology of spiders. Third edition. Oxford University Press, New York. 419 pp.

Galiano ME 1975 Nota sobre los pelos escamosos de Salticidae (Araneae). – Physis, Buenos Aires (C) 34: 215-217

Griswold CE, Ramírez MJ, Coddington J & Platnick NI 2005 Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. – Proceedings of the California Academy of Sciences 56 (4), Supplement II: 1-324

Hill DE 1979 The scales of salticid spiders. – Zoological Journal of the Linnean Society 65: 193-218 – doi: 10.1111/j.1096-3642.1979.tb01091.x

Lehtinen PT 1967 Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. – Annales Zoologici Fennici 4: 199-468

Lehtinen PT 1975a The significance of hair ultrastructure in phylogenetic classification of spiders. – Journal of Ultrastructure Research 50: 362-395

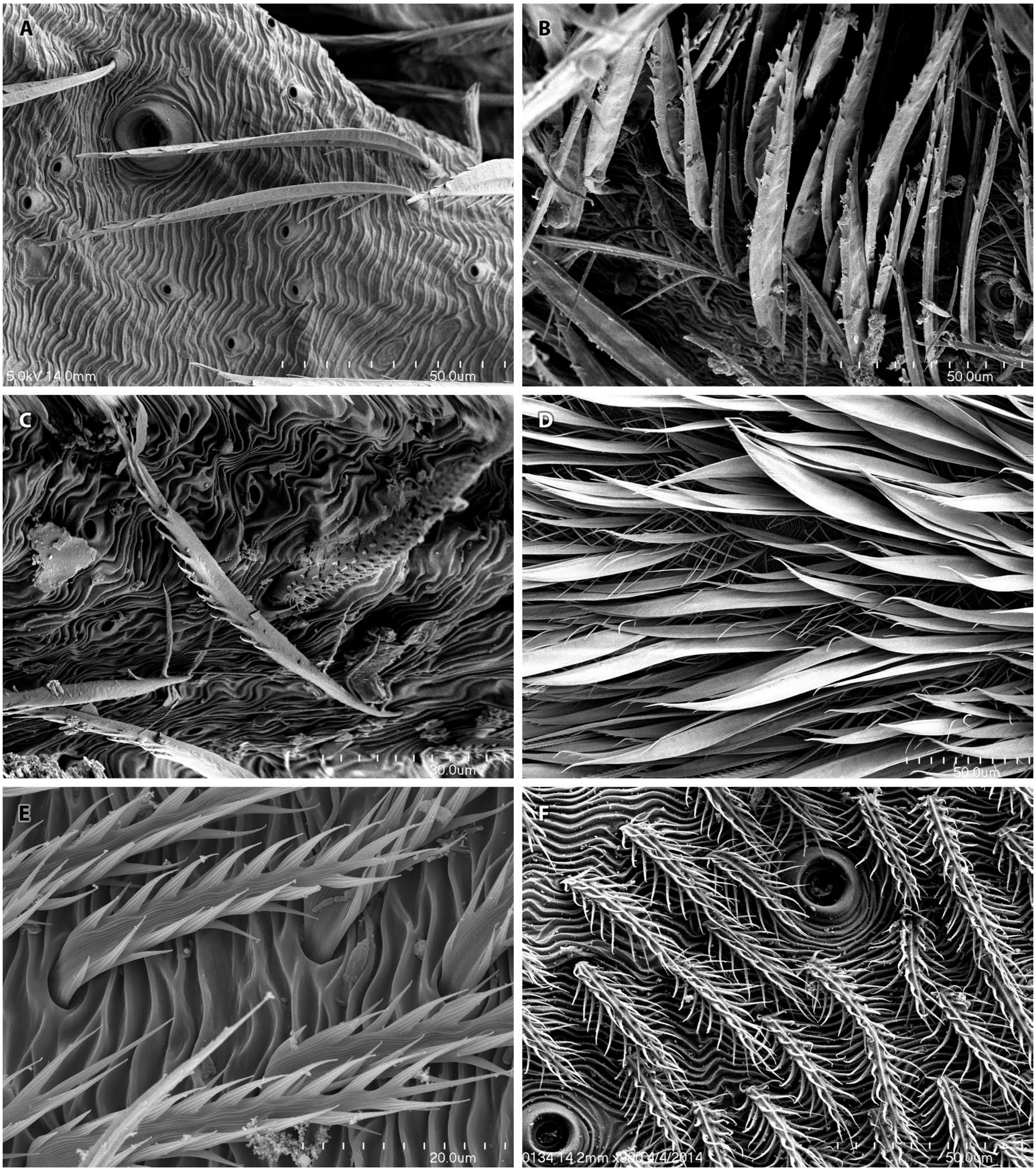

Fig. 6: Sicate setae on the abdomen (A, B, C), lanceolate setae on the abdomen (D), pinnate setae on the abdomen (E), arborate setae on the abdomen (F). **A.** *Cesonia bilineata*, **B.** *Herpyllus propinquus*, **C.** *Litopyllus temporarius*, **D.** *Scotophaeus blackwalli*, **E.** *Gnaphosa taurica*, male (photo Martin Ramírez), **F.** *Fedotovia uzbekistanica*.

Lehtinen PT 1975b Notes on the phylogenetic classification of Araneae. – Proceedings of the 6th International Arachnological Congress (Amsterdam 1974): 26-29, Pl. 1-4

Murphy J 2007 Gnaphosid genera of the world. British Arachnological Society, St. Neots, Cambs. 605 pp.

Ovtsharenko VI 1983 Spiders of the family Gnaphosidae of the European part of the USSR and Caucasus. Dissertation, Zoological Institute of the Academy of Science of the USSR, Leningrad, 24 pp.

Ovtsharenko VI 1985 Cuticular microstructure of the spider family Gnaphosidae (Aranei) and its use in the systematics. – Proceedings of the Zoological Institute of the USSR Academy of Science 139: 27-35

Ovtsharenko VI 1989 [Microstructures on the cuticle of the spiders of the family Gnaphosidae (Arachnida, Aranei)]. In: Lange AB (ed.) [The fauna and ecology of spiders and scorpions. Collection of arachnological papers]. Nauka Publishers, Moscow. pp. 5-14 [in Russian]

Ovtsharenko VI, Levy G & Platnick NI 1994 A review of the ground spider genus *Synaphosus* (Araneae, Gnaphosidae). – American Museum Novitates 3095: 1-27

Ovtsharenko VI & Platnick NI 1995 On the Australasian ground spider genera *Anzacia* and *Adelphodrassus* (Araneae, Gnaphosidae). – American Museum Novitates 3154: 1-16

Ovtsharenko VI, Platnick NI & Marusik YM 1995 A review of the Holarctic ground spider genus *Parasyrisca* (Araneae, Gnaphosidae). – American Museum Novitates 3147: 1-55

Platnick NI 1975 A revision of the Holarctic spider genus *Callilepis* (Araneae, Gnaphosidae). –American Museum Novitates 2573: 1-32

Platnick NI, Ovtsharenko VI & Murphy JA 2001 A review of the ground spider genus *Scotognapha* (Araneae, Gnaphosidae), and its radiation on the Canary and Salvage Islands. – American Museum Novitates 3338: 1-22 – doi: 10.1206/0003-0082(2001)338<0001:AROTGS>2.0.CO;2

Ramírez MJ 2014 The morphology and phylogeny of Dionychan spiders (Araneae: Araneomorphae). – Bulletin of the American Museum of Natural History 390: 1-374 – doi: 10.1206/821.1

Simon E 1893 Histoire naturelle des araignées. Deuxième édition. Part 1 (2). Roret, Paris. pp. 257-488

Townsend VR Jr & Felgenhauer BE 1998a Cuticular scales of spiders. – Invertebrate Biology 117: 318-330 – doi: 10.2307/3227034

Townsend VR Jr & Felgenhauer BE 1998b The cuticular scales of lynx spiders (Araneae, Oxyopidae). – Journal of Morphology 236: 223-231 – doi: 10.1002/(SICI)1097-4687(199806)236:3<223::AID-JMOR5>3.0.CO;2-3

Townsend VR Jr & Felgenhauer BE 1999 Ultrastructure of the cuticlar scales of lynx spiders (Araneae, Oxyopidae) and jumping spiders (Araneae, Salticidae). – Journal of Morphology 240: 77-92 – doi: 10.1002/(SICI)1097-4687(199904)240:1<77::AID-JMOR6>3.0.CO;2-P

Townsend VR Jr & Felgenhauer BE 2001 Phylogenetic significance of the morphology of the cuticular scales of the lynx spiders (Araneae: Oxyopidae). – Journal of Zoology 253: 309-332 – doi: 10.1017/S0952836901000292