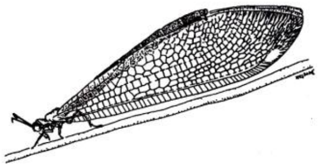

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Ultrastructural morphology of leg cuticle derivatives useful for phylogenetic study of Neuropterida (Insecta: Megaloptera, Neuroptera): preliminary report

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Abstract. Ultrasculpture of leg surface and cuticle derivatives such as spinules, sensilla, and spurs were investigated with SEM in the Neuropterida families Corydalidae and Sialidae (Megaloptera); Ascalaphidae, Chrysopidae, Dilaridae, Hemerobiidae, Ithonidae, Mantispidae, Myrmeleontidae, Nemopteridae, Nevrorthidae, Osmylidae, Polystoechotidae, Psychopsidae, and Sisyridae (Neuroptera). These characters may provide useful phylogenetic information for Neuropterida. The polarity of twenty-five character states of the tibio-tarsal area of the hind leg is preliminary determined. True spurs were not detected in Sisyridae examined.

Key words: Neuropterida, Megaloptera, Neuroptera, SEM, cuticle derivatives, microsculpture (texture) of leg surface, external morphology, spinules, sensilla, spines, spurs

Introduction

Characters of leg cuticle derivatives have recently been found to be useful in phylogenetic analyses of some Holometabolian orders (Basibuyuk & Quicke, 1995; Basibuyuk *et al*., 2000; Baszio & Richter, 2002; Vshivkova *et al*. 2007, 2009). The possible value of the ultrastructure morphology of sensilla, spines, and spurs is also obvious for palaeontology, palaeoecology, and taxonomy, which often use insect body fragments. However, neuropterologists' attention has been almost exclusively concentrated to the presence, number, shape and size of spurs. These characters have been discussed at least passing mention in many publications on Neuroptera (e.g., Tillyard, 1919; Tjeder, 1959, 1960, 1986; Hölzel, 1975, 1999; New, 1981, 1983, 1984a, 1985a,b; Penny, 1983, 1996; Mansell, 1985, 1990, 1992; Stange, 1989, 2008; Brooks & Barnard, 1990; Willmann, 1990; Oswald, 1993, 1998; Aspöck & Aspöck, 1997; Engel, 2002; Archibald & Makarkin, 2004; Penny & Winterton, 2007; Miller, 2008).

However, apart from these brief instances, leg cuticle vestiture and the external morphology of spurs, spines, and sensilla have received very little attention in Neuropterida. We know only few references where they have been treated in any detail. For example, Killington (1936) mentioned that tibial spurs of Osmylidae "are peculiar in being densely clothed with stiff hairs." Poivre (1978, 1981) described and schematically illustrated the tibial spur vestiture in some species of Mantispidae. Further, the ultrastructure of leg sensilla with regards to vibration communication in Neuropterida (particularly Chrysopidae) has received some attention (e.g., Devetak, 1998; Devetak *et al*., 1996, 2004).

Here, we report preliminary results of a study of the external morphology of leg cuticle derivatives in the majority of the neuropterid families, mainly to determine any phylogenetic significance of variation. We have paid particular attention to the tibio-tarsal area of the hind legs.

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Material and methods

Three species of Megaloptera (two families) and 15 species of Neuroptera (13 families) from Entomological Collections of the Institute of Biology and Soil Sciences, Russia (IBSS) were studied using scanning electron microscopy: MEGALOPTERA: Corydalidae: Chauliodinae gen. sp. (Thailand), *Protohermes martynovae* Vshivkova, 1995 (Russian Far East: Primorye); Sialidae: *Sialis* sp. (Primorye); NEUROPTERA: Ascalaphidae: *Ascalohybris subjacens* (Walker, 1853) (Japan: Kyusyu), *Libelloides sibiricus* (Eversmann, 1850) (Primorye); Chrysopidae: *Chrysopa intima* McLachlan, 1893 (Russian Far East: Khabarovski Krai), *Nineta alpicola* Kuwayma, 1936 (Primorye); Dilaridae: *Dilar septentrionalis* Navás, 1912 (Primorye); Hemerobiidae: *Micromus paganus* (Linnaeus, 1767) (Russia: Transbaikalia); Ithonidae: *Ithone fusca* Newman, 1838 (Australia); Mantispidae: *Mantispa floridana* Banks, 1897 (USA: Florida); Myrmeleontidae: *Dendroleon jezoensis* Okamoto, 1910 (Primorye); Nemopteridae: *Nemoptera sinuata* Olivier, 1811 (Armenia); Nevrorthidae: *Nipponeurorthus pallidinervis* Nakahara, 1958 (Japan: Kyusyu); Osmylidae: *Lysmus harmandinus* (Navas, 1910) (Primorye); Polystoechotidae: *Polystoechoetes punctata* (Fabricius, 1793) (USA: California); Psychopsidae: *Balmes* sp. (China); Sisyridae: *Climacia areolaris* (Hagen, 1861) (USA: Florida).

Both dry pinned specimens and ethanol preserved material were employed. The hind legs were removed (the right hind legs only used for microphotographs) and transferred to 98% ethanol, rinsed once, then air dried and mounted on a microscope stub prior to sputter coated with gold/platinum. Specimens were examined using a ZEISS EVO40 Scanning Electron Microscope.

The terminology used here for the general leg structures and derivatives follows that of Snodgrass (1993); and for the details of sensilla, spines, and spurs follows Altner (1977), Hallberg and Hansson (1999), Baszio and Richter (2002), and Vshivkova *et al.* (2007). We propose the following new terms describing leg cuticle: *peritheca*, the circular adjoining cuticle around the *theca* (the opening in the cuticle from which the sensillum is raised), which is either elevated above the surrounded cuticle (mound-like peritheca) or flat with it; and *perithecal process*, for the thorn-like outgrowth of the peritheca. For the purposes of this paper, the terms ventral, dorsal, and lateral are used with respect to the leg, i.e., ventral and dorsal indicate the lower and upper side of the leg derivatives relative to the surface of tibia and tarsus, lateral refers to the sides of the derivatives.

SEM was used to examine the microstructure of hind leg tibio-tarsal regions (Fig. 1), in particular, the apical (distal) tibial area, and the basal basitarsal area (Figs. 2, 3). The cuticle surface of some of the basitarsal area near the tibial spur attachment is often very different from the surrounded cuticle in having a denser, ribbed, spinulate, or wart-like vestiture, and it is termed here the *basitarsal rough area* or *basitarsal pad* (Figs. 5, 6).

Results and discussion

I. Ultramorphology of the cuticle surface (surface texture)

The outer surface of the cuticle, the epicuticula, is the thin non-cellular layer. Its texture throughout the tibio-tarsal area including spines and spurs is seldom plain, smooth or bare (Figs. 3, 5); it often has a wavy (corrugated) (Fig. 4) or wrinkled structure (Figs. 32, 33, 37, 45). It bears various irregular or regular ribs or ridges (Fig. 11), scale- or tile-like (polygonal) structures (Figs. 39, 42), wart- or pimple-like protuberances (Fig. 6), or different types of non-cellular (nodules, spinules, small spines) or cellular projections such as multicellular (spines, or spine-like structures) or unicellular (different sensilla) processes.

The cuticle of the basitarsal rough area (basal basitarsus) strongly differs from that of other portion of the tibio-tarsal area, particularly characterized by a denser cover of non-cellular formations, which consists of ordinary (Fig. 32) or modified spinules (Figs. 3, 7–9, 36, 44), ribs (Fig. 10), or warts (which tend to be scales distally) (Figs. 5, 6).

II. Spinules

Spinules (or "microtrichia") are non-cellular, non-innervated, non-socketed, and non-articulated minute cuticle processes. Three types of spinules are distinguished according their location in tibio-tarsal area: (1) ordinary spinules, (2) spinules of the basitarsal rough area, and (3) spur spinules.

Ordinary spinules. The leg surface is covered with ordinary spinules, which usually spread uniformly throughout the surface (Figs. 4, 21). The ordinary spinules may completely cover the entire tibio-tarsal area (e.g., Megaloptera, Dilaridae, Mantispidae, Nevrorthidae, Psychopsidae, Sisyridae; Fig. 2), or partially disappear in the apical (distal) portion of the tibia (e.g., Chrysopidae, Hemerobiidae; Fig. 7), or are absent in most portion of tibia and tarsus (e.g., Ascalaphidae, Ithonidae, Myrmeleontidae, Nemopteridae, Osmylidae, Polystoechotidae; Figs. 5, 10, 31). They are trichoid (many neuropterids; Figs. 3, 4, 24, 25) or thorn-like structures (e.g., Dilaridae; Figs. 21–23). The external morphology of ordinary spinules is usually the same throughout entire tarso-tibial area.

Basitarsal rough area spinules. These spinules may be trichoid (Figs. 3, 43), spine-like or pyramidal-like projections with a short or long tapering apex (Figs. 7, 8) or flattened, triangle-like with a weakly or strongly protruding apex (Fig. 9). Spinules of the basitarsal rough area are the same as the ordinary spinules only in Megaloptera and Nevrorthidae (*Nipponeurorthus pallidinervis*) (Fig. 3); these spinules differ in other neuropterids examined. They are usually weaker developed at the base of the basitarsal rough area and become longer in the central and apical portions.

Spur spinules. Spinules on the spur surface vary from simple needle-like projections (e.g., Sialidae; Figs. 34, 35) to the very developed scale-like outgrowths (e.g., Nevrorthidae, Osmylidae, Psychopsidae; Figs. 47–50). They cover the entire spur body except the very basal and apical portions. Scale-like spinules may lie tightly against the spur body (Fig. 47) or at an angle to it, in this case the spurs have a pine cone-like appearance (Figs. 49, 50).

III. Sensilla

All sensilla detected in the tibio-tarsal area were setiform; campaniform, coeloconicum or other non-trichoid sensilla were not found.

Many different names have been applied to setiform sensilla despite similarity in form and external morphology. Altner (1977) proposed a classification based on the presence/absence and structure of the pores. According to this classification, all sensilla may be grouped into three major groups: poreless (NP), wall-pore single-walled (subtype SW) and wall-pore double-walled (subtype DW), and terminal pore sensilla (TP). The most common types of setiform sensilla can be defined as (I) trichoid (SWtrh) sensilla with a long shaft, a low number of sensory cells (1-3), usually with unbranched dendrites, and comparatively thick cuticle with a low pore density; (II) basiconic (SWbsc) sensilla usually with a short shaft, a low number of sensory cells (1-3), branched dendrites, and a thin cuticle with high pore density; (III) chaetic (TP) sensilla with a long shaft, an apical pore, 4-5 sensory cells one of which is mechanosensory and four are gustatory; (IV) poreless chaetic sensilla. Some non-setiform sensilla are also recognized (Hallberg & Hansson, 1999). The majority of setiform sensilla (single-walled and poreless) appear to be mechanosensory. Setiform sensilla with a long shaft and an apical pore are functioning collectively as mechanosensory and gustatory organs. Wall-pore sensilla with numerous pores (e.g., sensilla basiconica) are known as chemoreceptors (olfaction, gustation). In spite of such detailed classification, problem distinguishing types of setiform sensilla still exist because the pores are often not visible even with SCAN or TEM examination.

Based on size, shape, and external ultramorphology, five types and subtypes of sensilla were identified in the tibio-tarsal area:

Type A. Sensilla chaetica (perhaps, poreless). These are basic, ordinary sensilla of the tibio-tarsal area in almost all studied neuropterids except some Ascalaphidae (Fig. 5) and Nemopteridae.

1. **Subtype t-ss I:** long sensilla, arising from flexible sockets, with the seta trunk gradually tapering and a sharp apex. They are straight or slightly curved and sit in openings (theca) surrounded by a more or less developed bulb-like (Figs. 14, 17) or pitcher-like base (peritheca) (Figs. 21, 22) formed by a joint membrane. These sensilla are distinguished from sensilla t-ss II subtype by larger shaft size (as much as 2-3 times) and larger socket. They are longitudinally grooved (Figs. 14, 18, 24, 25) with weakly (e.g., Chauliodinae; Fig. 17) or well-developed ridges; the ridges are usually non-serrate (Figs. 14, 16, 25), or may be slightly notched (Fig. 22), especially distally. The number of sensillum ridges varies from 6 (*Balmes* sp.), 10 (*Dilar septentrionalis*) to 12–16 (e.g., Megaloptera; *Mantispa floridana*, *Micromus paganus*). Each sensillum ridge is directed from the base to the apical portion (Figs. 18, 22), sometimes merged with each other (Fig. 23).

The peritheca of sensilla chaetica in some neuropterid families has a spine-like perithecal process, which may be short (less than the sensillum diameter at its base) (*Lysmus harmandinus*, *Balmes* sp., *Chrysopa intima*) (Figs. 14, 23, 25) or long (longer than the sensillum diameter at its base) (*Micromus paganus*, *Climacia areolaris*) (Figs. 28–31). This perithecal process probably restricts the backward mobility of the sensilla. A similar structure was observed in some Hymenoptera sensilla ("spur of STB socket") (Basibuyuk *et al*., 2000); however, the homology of those "spurs" with spine-like perithecal process described here is uncertain.

2. **Subtype t-ss II:** sharp-tipped, setiform sensilla, which differ from the t-ss I subtype by being shorter and more slender, and in having a less developed socket.

3. **Subtype t-ss III:** spine-like, thick, robust, and blunt-tipped sensilla. This type of sensilla appears to be numerous in Ascalaphidae and Nemopteridae examined, especially on the tarsal surface of *Libelloides sibiricus* (Fig. 5). The long, medium and short spine-like sensilla are distinguished by their size.

4. **Type B**. Sensilla trichodea: stright, pointed, longitudinally grooved (Figs. 10, 14, 15), smaller than sensilla chaetica distinguishing from the latter by a weakly developed peritheca; these occur rarely, and then in the apical tibial area. This type is characterized by the absence of a perithecal process, even in those taxa in which the ordinary chaetic sensilla posses such projection (Fig. 14); they are usually lighter at SEM observation in comparison with ordinary chaetic sensilla.

5. **Type C**. Sensilla basiconica: markedly shorter than sensilla chaetica, slightly curved (Figs. 17, 19, 26), peg-like, blunt-tipped sensilla with an obvious pimple at the apex (Fig. 20). The sensilla wall is longitudinally grooved and slightly transversally wrinkled; the surface appears to have pores. Such sensilla are rarely found in the apical tibial area, but more often on tarsal segments.

IV. Spines

Spines are multicellular cuticle processes. Some of them are solidly fixed to the surrounded cuticle (immovable spines) and some are set in openings surrounded by the perithecal ring and, probably, partially movable (socketed spines). Immovable spines may independently arise from the epicuticula surface or be a projection of other structures such a perithecal process of some neuropterid sensilla chaetica (Figs. 29, 30). The tibio-tarsal socketed spines remind ordinary sensilla chaetica in general structure and external morphology being, however, thicker and having somewhat different perithecal morphology (Figs. 10, 13, 18). Socketed spines differ from tibial spurs in having longitudinal ridges and in the absence any scattered spinules or setiform sensilla.

The spines located at the base of apical tibial spurs (usually one or two in number) are termed falsicalcar/falsicalcarae (or false spurs) (Vshivkova *et al*., 2007). In *Climacia areolaris* (Sisyridae) two falsicalcarae are found to present sitting in well-formed sockets looking like spurs (Fig. 43), while true hind tibial spurs in this species were not detected.

V. Spurs

Spurs are spine-like, multicellular processes, which are only present on the tibia, therefore they are often named "tibial spurs". In Neuropterida there are only apical (distal) spurs, while some other holometabolian orders also possess subapical spur/ spurs. They are located ventrally at the apical edge of the tibia, which is separated from the first tarsal segment (basitarsus) by a more or less visible joint membrane; the spurs are inserted in the membrane and often appear as structures roofed by the apical tibial edge. The number of spurs varies from 0 to 2. The spur formula is 2.2.2 if maximal number of spurs is present in each leg.

Tibial spurs are present in almost all families of Neuropterida. We could not detect them in *Dilar septentrionalis* (Dilaridae), *Nemoptera sinuata* (Nemopteridae), and *Climacia areolaris* (Sisyridae). Any data on the presence/ absence of spurs in Dilaridae are absent in the literature. Small spurs are sometimes present in Nemopteridae (Hölzel, 1975, 1999). As to Sisyridae, it was widely accepted that spurs are present in this family, i.e., one spur on the distal end of the prothoracic tibia and two on the distal ends of the meso- and metathorasic tibiae (Killington, 1936; Parfin and Gurney, 1956; Riek, 1975). However, we found that at least the metathorasic tibiae of *Climacia areolaris* have socketed spines (falsicalcarae, see above), not true spurs (Fig. 43). In many subfamilies, tribes, or genera, spurs are also absent (e.g., Berothidae: *Nosybus* Navás, *Stenobiella* Tillyard, *Spermophorella* Tillyard, *Trichoma* Tillyard; Coniopterygidae: Brucheiserinae; Hemerobiidae: *Zachobiella* Banks; Ithonidae: *Rapisma* McLachlan; Myrmeleontidae: *Fenestroleon* New, tribe Dendroleontini; Nymphidae: *Myiodactylus*-group) (Tillyard, 1916; Rick, 1975; Barnard, 1981; New, 1984b).

If two spurs are present, one is anterior (inner) and the other posterior (outer). In many neuropterids, both spurs are usually of the same size and length (Figs. 3, 34, 44, 48). Sometimes the anterior spur may be larger than the posterior (Fig. 36). Anterior and posterior spurs may be similar in shape or different (e.g., *Ascalohybris subjacens*, *Libelloides sibiricus*). Spurs of most neuropterids are usually straight and conical (Figs. 5, 32, 34, 46), but, some are slightly curved. Some neuropterids are characterized by very strongly arched spurs with a sub-basal prominence, i.e., "hooked spurs" (e.g., Myrmeleontidae: Acanthaclisinae) (New, 1985a).

Spur texture may be almost smooth (*Chrysopa intima*; Fig. 46), slightly (e.g., *Micromus paganus*; Figs. 44, 45) or strongly wrinkled in the central (e.g., Corydalidae; Figs. 32, 33) or distal portion (e.g., *Polystoechoetes punctata*; Fig. 37). Spur surface may be polygonal (e.g., Ascalaphidae, Fig. 42) or scaled in texture (e.g., Ithonidae; Fig. 39). Different projections are developed in other neuropterids: needle-like spinules (Sialidae; Fig. 34); more or less developed scale-like projections tightly adjoining the spur body (*Nipponeurorthus pallidinervis*, Fig. 48) or at an angle to the spur body (*Balmes* sp.; Figs. 49, 50). Spur surface in different neuropterids usually possesses similar ultramorphology (Figs. 12, 37, 42), however the dorsal surface may have more developed microsculpture or denser spinulate cover; the apices of spurs are usually devoid of microprojections. The ventral portion of both spurs in *Dendroleon jezoensis* (Myrmeleontidae) bear a thin, sharp longitudinal blade from base to apex (Figs. 40, 41).

Characters potentially useful for phylogenetic purpose

All leg cuticle derivatives (non-cellular, unicellular and multicellular) are directed apicad as if brushed in this way. The tibio-tarsal areas of Megaloptera and Neuroptera examined have some shared principal features: (1) development of non-cellular vestiture on the leg cuticle surface; (2) presence of the basitarsal rough area; (3) presence of numerous longitudinally grooved sensilla chaetica with non-serrate or slightly serrate ridges and fewer setiform sensilla of other types (trichodea, basiconica); (4) spines possess non-serrate or slightly serrate longitudinal ridges; and (5) non-sensillate spurs, which lack toothed rim/rims.

The differences in leg derivatives are probably characteristic of families and genera, and therefore carry a phylogenetic signal. Below, the polarities determined for the twenty-five identified characters found in the tibio-tarsal area of the hind leg are listed, coded “(0)” for putative primitive (plesiomorphic) state, and “(1)” to “(3)” for putative advanced (apomorphic) states. This evaluation should be considered preliminary and requires further investigation of other neuropterid taxa, and other holometabolous orders to confirm its accuracy. Some of characters are multi-state; however, we do not presently propose any transformation series because of incomplete data. Nevertheless, these characters may be used as an additional source of phylogenetic information together with characters of the larvae, genitalia of imagoes (e.g., Aspöck *et al*., 2001), and molecular data (e.g., Haring & Aspöck, 2004).

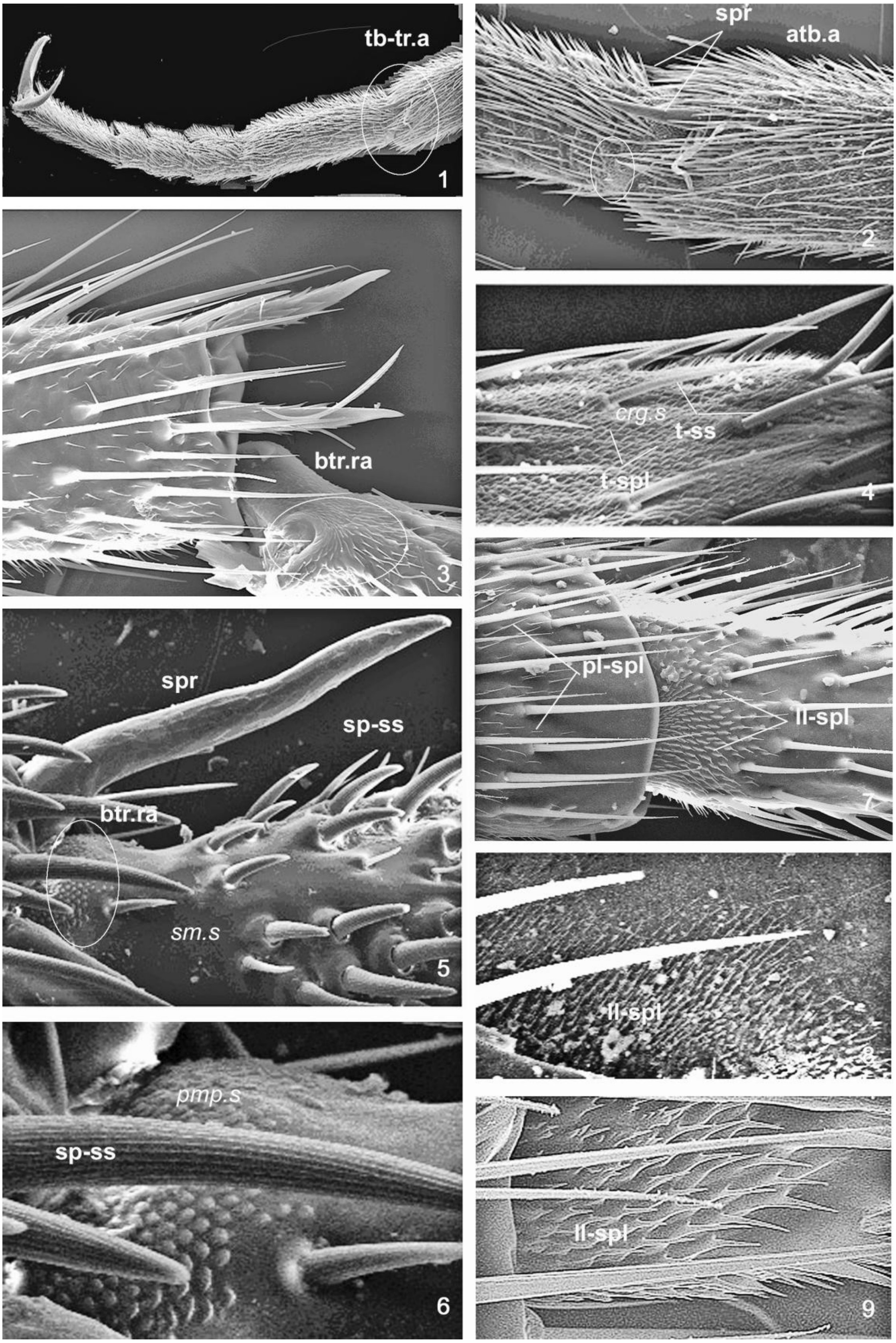
Cuticle surface texture and non-cellular vestiture

Character 1: Surface texture of tibio-tarsal area.
(0) slightly wrinkled (e.g., Megaloptera; Osmylidae; Figs. 2, 32);
(1) strongly wrinkled, or wavy (corrugated) (e.g., Mantispidae; Fig. 4);
(2) more or less plain, smooth (often non-spinulate) (e.g., Ascalaphidae, Chrysopidae, Dilaridae, Myrmeleontidae, Polystoechotidae; Figs. 5, 10).

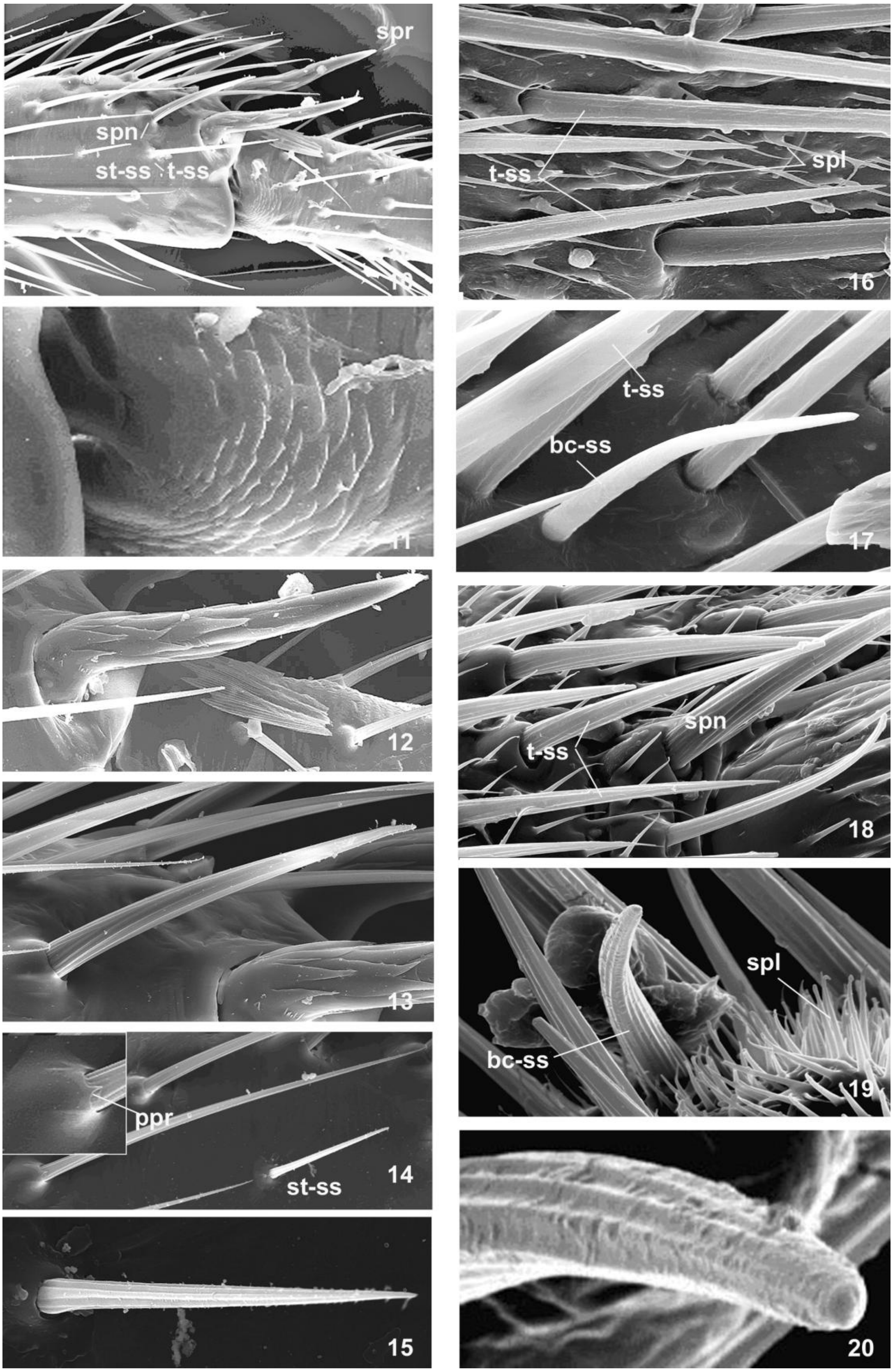
Character 2: Non-cellular vestiture of tibio-tarsal area.
(0) uniformly covered by spinules (e.g., Megaloptera, Dilaridae, Mantispidae, Nevrorthidae, Psychopsidae, Sisyridae; Figs. 3, 4, 14, 50);
(1) spinules absent at apical (distal) portion of tibia and basitarsal area (e.g., Chrysopidae, Hemerobiidae; Figs. 7, 44);
(2) spinules absent over most of tibio-tarsal area (e.g., Ascalaphidae, Ithonidae, Myrmeleontidae, Nemopteridae, Osmylidae, Polystoechotidae; Figs. 5, 10).

Character 3: Non-cellular vestiture of basitarsal rough area.
(0) covered with spinules similar to ordinary spinules (e.g., Megaloptera, Nevrorthidae; Figs. 2–3);
(1) covered with spinules different from ordinary spinules (e.g., Chrysopidae, Ithonidae, Hemerobiidae; Figs. 7–9, 44);
(2) covered by non-spinule formations (ribs, or pimple-like, or scale-like protuberances) (e.g., Osmylidae, Ascalaphidae; Figs. 6, 11).

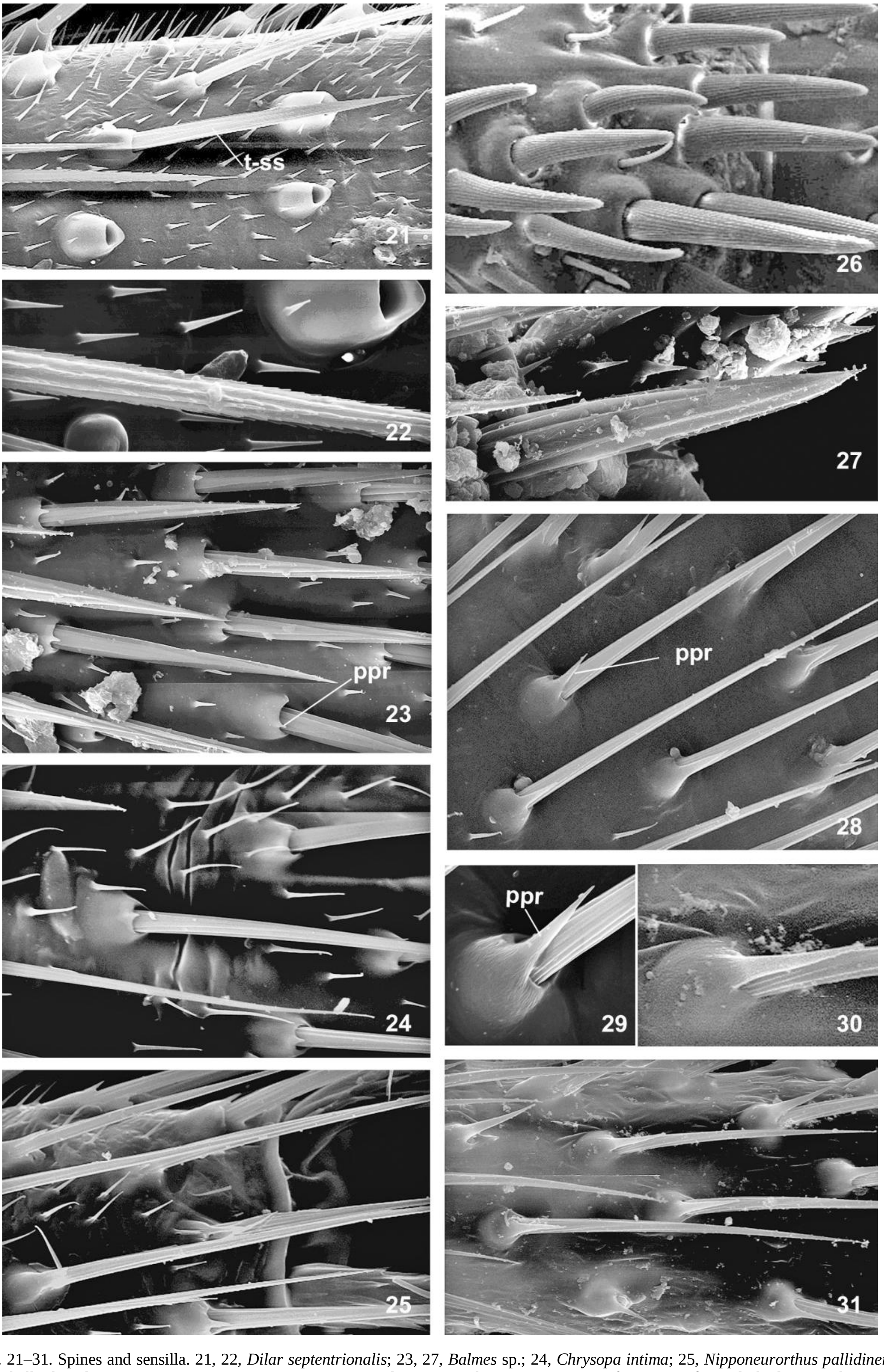
Character 4: Spinulate vestiture of basitarsal rough area.
(0) covered with trichoid spinules having similar size with ordinary spinules (e.g., Megaloptera, Nevrorthidae; Figs. 3, 32);



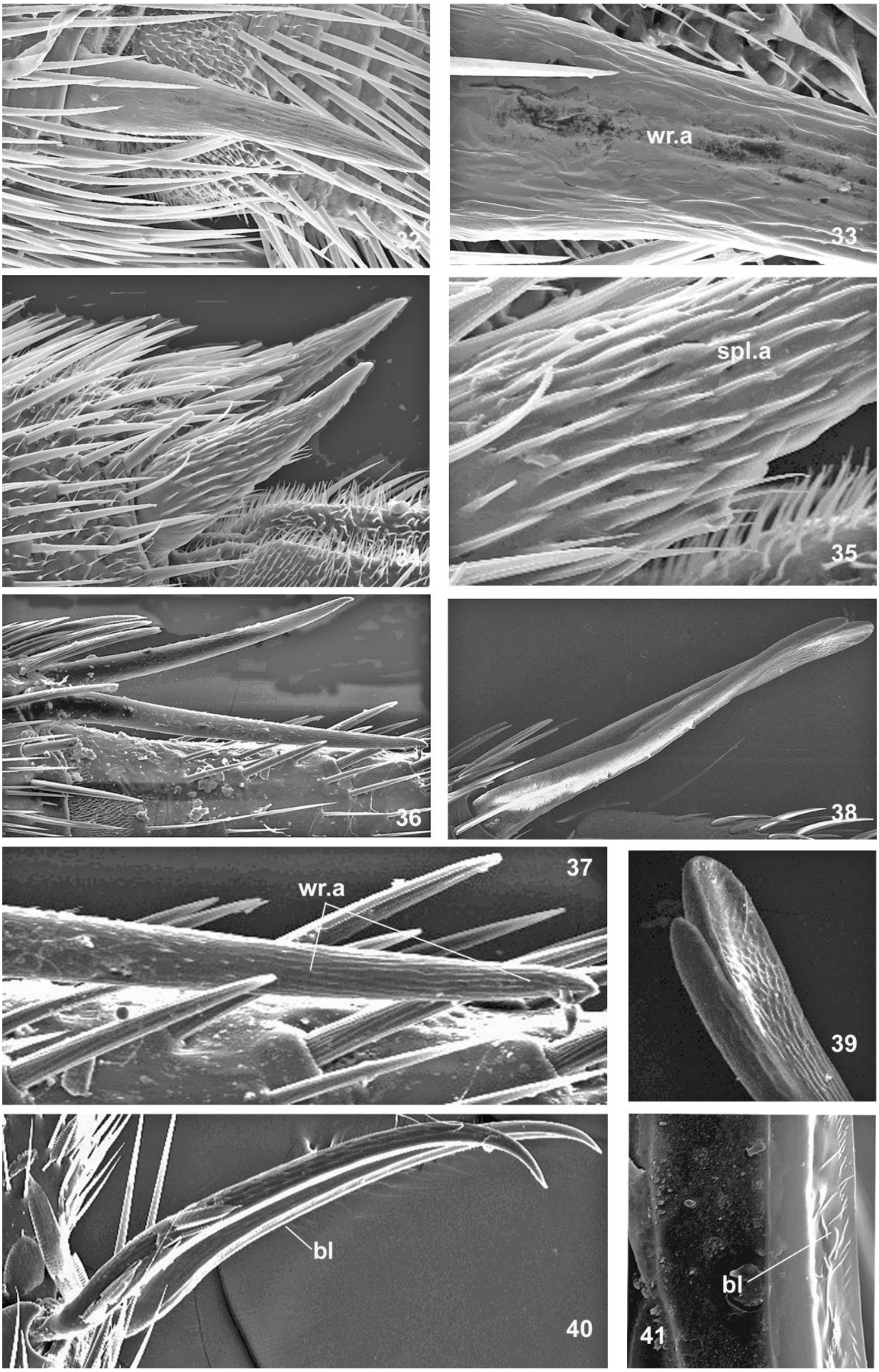
Figs. 1–9. Neuropterida leg surface and cuticle derivatives: spinules, spines, spurs. 1, 2, Chauliodinae gen. sp.; 3, *Nipponeurorthus pallidinervis*; 4, *Mantispa floridana*; 5, 6, *Libelloides sibiricus*; 7, *Nineta alpicola*; 8, *Ithone fusca*; 9, *Micromus paganus*. 1, tarsus and apex of tibia, 2, 3, 5, 7, tibio-tarsal area; 4, apical (distal) portion of tibia; 6, 8, 9, proximal portion of basitarsus (basitarsal rough area). *atb.a*, apical tibial area; *btr.ra*, basitarsal rough area; *crg.s*, corrugated surface; *ll-spl*, spinules of basitarsal area; *pl-spl*, long trichoid ordinary spinules; *pmp.s*, pimpled surface; *tb-tr.a*, tibio-tarsal area; *sp-ss*, spine-like sensilla; *sm.s*, smooth surface; *spr*, spur; *t-spl* - short trichoid ordinary spinules; *t-ss*, sensilla chaetica.



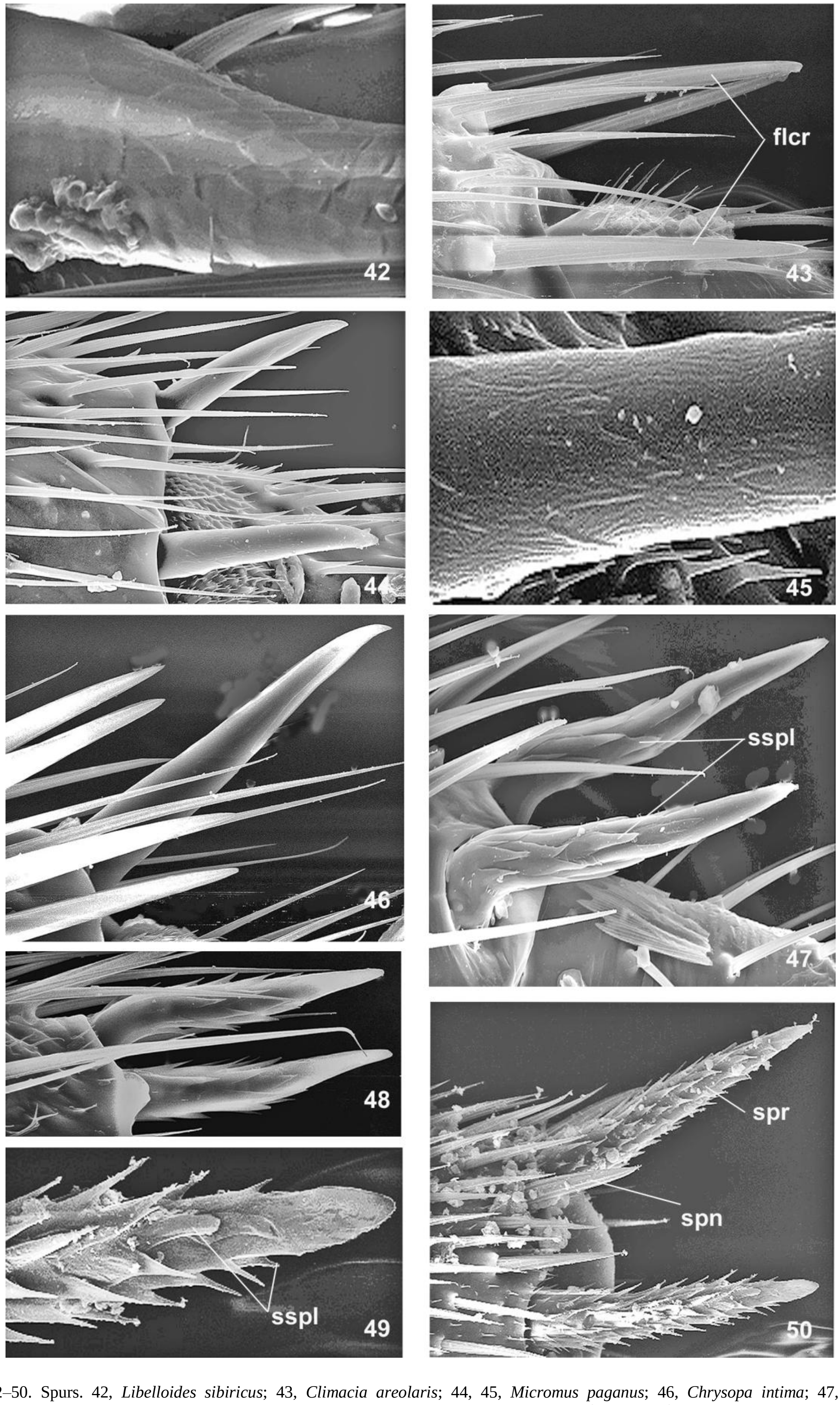
Figs. 10–20. Leg surface, sensilla, and spines. 10–15, *Lysmus harmandinus*; 16, 17, Chauliodinae gen. sp.; 18–20, *Sialis* sp.; 10, tibio-tarsal area; 11, basitarsal rough area; 12, tibial spur; 13, tibial spine; 14, sensilla chaetica and sensillum trichodea; 15, sensillum trichodea; 16, sensilla chaetica and ordinary spinules; 17, sensillum basiconica and basal portions of sensilla chaetica; 18 – sensilla chaetica and spine; 19, 20, sensillum basiconica and its apical portion. *bc-ss*, sensillum basiconica; *ppr*, perithecal process; *spl*, ordinary spinule; *spn*, spine; *spr*, spur; *st-ss*, sensillum trichodea; *t-ss*, sensillum chaetica.



Figs. 21–31. Spines and sensilla. 21, 22, *Dilar septentrionalis*; 23, 27, *Balmes* sp.; 24, *Chrysopa intima*; 25, *Nipponeurorthus pallidinervis*; 26, *Libelloides sibiricus*; 28, 29, *Micromus paganus*; 30, 31, *Climacia areolaris*. 21–25, 28–31, fragments of apical tibial area with spinules, sensilla; 26, basitarsus with spine-like sensilla and sensilla basiconica; 27, spine. *ppr*, perithecal process; *t-ss*, sensillum chaetica.



Figs. 32–41. Spurs. 32, 33, Chauliodinae gen. sp.; 34, 35, *Sialis* sp.; 36, 37, *Polystoechotes punctata*; 38, 39, *Ithone fusca*; 40, 41, *Dendroleon jezoensis*. 32, 34, 36–38, apical (distal) tibial spurs; 33, 35, medial portion of spurs; 37, 39, apical portion of spurs; 41, blade of spur. *rgs.s*, wrinkled (rugose) surface of spur.



Figs. 42–50. Spurs. 42, *Libelloides sibiricus*; 43, *Climacia areolaris*; 44, 45, *Micromus paganus*; 46, *Chrysopa intima*; 47, *Lysmus harmandinus*; 48, *Nipponeurorthus pallidinervis*; 49, 50, *Balmes* sp.; 42, 45, medial portion of spur; 43, falsicalcarae; 44, 46–48, 50, tibial spurs; 49, apical portion of spur.

(1) covered with trichoid spinules markedly longer than ordinary spinules (e.g., Sisyridae; Fig. 43);
(2) covered with pyramidal outgrowths with tapering apical projection (e.g., Chrysopidae, Ithonidae; Figs. 7–8);
(3) covered with flattened, triangle-like projections with tapering apex (e.g., Hemerobiidae; Fig. 9).

Character 5: Shape of ordinary spinules.
(0) simple trichoid projection (i.e., thin, uniformly tapering to the apex; e.g., Chrysopidae, Nevrorthidae; Figs. 24, 25);
(1) thorn-like (e.g., Dilaridae; Fig. 21).

Sensilla

Character 6: Sensilla chaetica vestiture of tibio-tarsal area.
(0) distributed irregularly (Figs. 2, 10);
(1) distributed regularly (this character state is present in some mecopterids, not discovered yet in neuropterids examined).

Character 7: Spine-like sensilla vestiture of tibio-tarsal area.
(0) absent (e.g., Megaloptera; Chrysopidae, Mantispidae);
(1) present, rare (e.g., Polystoechotidae);
(2) present, numerous (may be more numerous than sensilla chaetica) (e.g., Ascalaphidae; Fig. 26).

Character 8: Number of chaetic sensilla ridges.
(0) about 14–16, or more (e.g., Megaloptera; Mantispidae; Fig. 18);
(1) about 10–12 ridges (e.g., Ascalaphidae, Chrysopidae, Dilaridae, Hemerobiidae, Myrmeleontidae, Nevrorthidae, Osmylidae, Polystoechotidae, Sisyridae; Fig. 9);
(2) less than 10 (e.g., Psychopsidae; Fig. 27).

Character 9: Shape of chaetic sensilla longitudinal ridges.
(0) non-serrate ridges (most neuropterids; Figs. 16, 24);
(1) weakly serrate, especially distally (e.g., Dilaridae; Fig. 22);
(2) strongly serrate (some Trichoptera) (Vshivkova *et al.*, 2007).

Character 10: Shape of chaetic sensilla peritheca.
(0) weakly developed, with slightly prominent wall (e.g., Corydalidae, Fig. 17);
(1) markedly prominent, bulb-like (e.g., Sialidae, most Neuroptera; Figs. 3, 14, 18, 23–25, 28-30);
(2) strongly prominent, pitcher-like (e.g., Dilaridae; Fig. 21).

Character 11: Perithecal process.
(0) absent (e.g., Megaloptera; many Neuroptera; Fig. 17);
(1) present (Psychopsidae, Chrysopidae, Osmylidae, Nevrorthidae, Hemerobiidae, Sisyridae; Figs. 14, 23, 24, 25, 29, 30).

Character 12: Size of perithecal process.
(0) short process (shorter than the sensilla diameter at the base) (e.g., Osmylidae, Chrysopidae; Figs. 14, 24);
(1) long process (longer than the sensilla diameter at the base) (e.g., Hemerobiidae, Sisyridae; Figs. 29–31).

Character 13: Sensilla basiconica.
(0) rare in the tibio-tarsal area (e.g., Corydalidae, most Neuroptera; Fig. 17);
(1) relatively numerous (e.g., Ascalaphidae, Fig. 26).

Socketed spines

Character 14: Longitudinal ridges of socketed spines.
(0) non-serrate (e.g., Megaloptera, most Neuroptera; Fig. 10);
(1) slightly serrate (e.g., Psychopsidae; Fig. 27);
(2) strongly serrate (some Trichoptera) (Vshivkova *et al*., 2007).

Character 15: Falsicalcarae.
(0) absent;
(1) present (Sisyridae; Fig. 43).

Spurs

Character 16: Hind tibial spur.
(0) two spurs present (Megaloptera, most Neuroptera examined);
(1) one spur present (Chrysopidae; Fig. 46);
(2) spurs absent (e.g., Sisyridae, Dilaridae, Nemopteridae examined; Fig. 43).

Character 17: Spur vestiture.
(0) non-spinulate (e.g., Corydalidae; Chrysopidae, Hemerobiidae, Ascalaphidae, Ithonidae; Figs. 32, 38–39, 42, 44–46);
(1) spinulate (e.g., Sialidae; Figs.12, 34, 47–50);

Character 18. Texture of spur surface.
(0) markedly wrinkled, at least in apical portion (e.g., Corydalidae; Polystoechotidae; Figs. 32, 37);
(1) smooth or slightly wrinkled (e.g., Hemerobiidae, Chrysopidae; Figs. 44–45, 46);
(2) polygonal (e.g., Ascalaphidae, Myrmeleontidae; Figs. 5, 40);
(3) tight scale-like (e.g., Ithonidae; Fig. 39).

Character 19. Shape of spur spinules.
(0) needle-like (e.g., Sialidae; Fig. 34);
(3) scale-like (e.g., Osmylidae, Nevrorthidae, Psychopsidae; Figs. 47-50).

Character 20: Spur relative size.
(0) both spurs almost equal size (e.g., Megaloptera; Hemerobiidae, Neurorthidae, Osmylidae, Psychopsidae; Figs. 3, 44, 47, 48, 50);
(1) anterior spur markedly longer than posterior (e.g., Polystoechotidae; Fig. 36).

Character 21: Texture of the basitarsal rough area (near the tibial spur attachment).
(0) spinulate; shape and size of spinules not strongly differ from ordinary spinules on tarsotibial surface (e.g., Megaloptera, Nevrorthidae (*Nipponeurorthus pallidinervis*) (Fig. 2);
(1) spinulate; spinules differ from ordinary spinules - larger, or with wider basement (Fig. 7);
(2) ribbed (Fig. 11);
(3) covered with pyramid, scale- or wart-like structures (Figs. 5, 6).

Character 22: Spur shape.
(0) straight, conical, (e.g., Hemerobiidae, Chrysopidae; Figs. 44, 46);
(1) at least one spur curved (e.g., Myrmeleontidae; Fig. 40);
(2) both spurs curved (arched) (e.g., Myrmeleontidae: Acanthaclisinae) (New, 1985a).

Character 23: Differentiation of spur dorsal and ventral portions.
(0) uniformly conical spurs with uniform vestiture (e.g., Megaloptera; most Neuroptera; Fig. 50);
(1) dorsal and ventral parts of spur are different in vestiture and shape (e.g., Myrmeleontidae; Fig. 41).

Character 24. Subapical prominence (tooth) of spur.
(0) no subapical tooth (Megaloptera, most Neuroptera);
(1) subapical tooth present (e.g., Myrmeleontidae: Acanthaclisinae) (New, 1985a).

Character 25: Spur blade formation.
(0) any blade or rim/rims absent;
(1) spur with developed blade (e.g., Myrmeleontidae; Figs. 40, 41).

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