Received: 30 April 2020 | Revised: 17 June 2020 | Accepted: 11 July 2020
DOI: 10.1002/jmor.21240

RESEARCH ARTICLE

JOURNAL OF morphology WILEY

Comparative study of sensilla and other tegumentary structures of Myrmeleontidae larvae (Insecta, Neuroptera)

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Funding information
Instituto de Biología, Universidad Nacional Autónoma de Mexico, Grant/Award Number: CT53/16-CT54/16; Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica, UNAM, Grant/Award Number: IN207517; Spanish Ministry of Sciences and Innovation, Grant/Award Number: CGL2010-22267-C07-05; Universidad Nacional Autónoma de México

Peer Review
The peer review history for this article is available at https://publons.com/publon/10.1002/jmor.21240.

Abstract

Antlion larvae have a complex tegumentary sensorial equipment. The sensilla and other kinds of larval tegumentary structures have been studied in 29 species of 18 genera within family Myrmeleontidae, all of them with certain degree of psammophilous lifestyle. The adaptations for such lifestyle are probably related to the evolutionary success of this lineage within Neuroptera. We identified eight types of sensory structures, six types of sensilla (excluding typical long bristles) and two other specialized tegumentary structures. Both sensilla and other types of structures that have been observed using scanning electron microscopy show similar patterns in terms of occurrence and density in all the studied species (with few exceptions). The sensilla identified are: coeloconica, placoidea, basiconica, trichodea type I, trichodea type II, and campaniformia. All these sensilla have mechano- or chemosensorial functions. Some regions of the larval body have been studied using SEM for the first time, such as the surface of the food canal, which bears sensilla coeloconica, and the abdominal segment X, that bears three types of sensilla: coeloconica, basiconica, and campaniformia. Sensilla placodea are newly reported on antlion larvae, being present on the mandibular base, pronotum, mentum, and cardum. Also, new locations of sensilla coeloconica (e.g., on rastra) and sensilla campaniformia (e.g., on odontoid processes) are noted. A novel porous texture with chemoreceptor function has been identified in the base of mandibles. A mechanism of dentate-notched surfaces that anchor maxillae and mandible, reinforcing the food canal, is detailed. All these sensorial structures, in addition to ocular tubercles for light caption and their great muscular system, confer to these larvae an extraordinary predation capacity to success hunting and living in such harsh environments.

KEYWORDS
antlion, chemoreceptor, mechanoreceptor, morphology, SEM

1 | INTRODUCTION

The family Myrmeleontidae, commonly known as antlions, is the most diverse family within the order Neuroptera. Although many recent studies have focused on the phylogeny of this group employing different sources of information (e.g., Badano, Aspöck, Aspöck, & Cerretti, 2017; Badano, Aspöck, Aspöck, & Haring, 2017; Jones, 2019; Michel et al. 2017), trying to understand the relation between antlions and owlflies, the lastest phylogenomic analyses (Machado et al., 2019; Winterton et al., 2018) finally include owlflies (formerly Ascalaphidae) in Myrmeleontidae (Machado et al., 2019; Winterton et al., 2018). With this inclusion, the family

Myrmeleontidae comprise 2,090 extant species (Oswald, 2020; Oswald & Machado, 2018).

This success is probably due to the specialization of larval stages, especially in those groups, which succeed in colonizing the inhospitable sandy environment and becoming true psammophilous (Badano & Pantaleoni, 2014; Mansell, 1999).

The phylogenetic relevance of larvae in the evolution of this group has been highlighted, and recent works related to this issue just corroborate it (Badano, Aspöck, Aspöck, & Cerretti, 2017; Badano, Engel, Basso, Wang, & Cerretti, 2018; Winterton et al., 2018).

Antlion larvae are well-known due to the fact that some species make pitfall traps in the sand (Badano, Aspöck, Aspöck, & Cerretti, 2017; Stange, 2004). This behavior, however, occurs in only a few of the genera, and most of them are ambush predators that remain completely still waiting for their preys.

Indeed, they can be found in many different habitats: tree cavities, caves, burrows, between stones, and so forth. Considering Myrmeleontidae sensu stricto, the majority of species live buried, or partly buried (keeping mandibles, ocular tubercles and sometimes also a part of the pronotum unburied), in substrates such as organic matter, debris, sand, and so forth (Badano & Pantaleoni, 2014; Mansell, 1999; Stange, 2004). As has already been commented, some groups have succeeded in becoming psammophilous by living completely buried in the sand. Therefore, it is not surprising that the body surface of Myrmeleontidae larvae is completely covered by setae which perform a mechanosensory function, among others (Badano & Pantaleoni, 2014; Devetak, Klokočovnik, Lipovšek, Bock, & Leitinger, 2013; Lipovšek Delakorda, Pabst, & Devetak, 2009). However, they also present other types of sensilla and cuticular sensorial structures that can only be observed by means of scanning electronic microscopy (SEM).

Cuticular sensilla are basically modified setae with sensorial functions (Chapman, 1998; Römer, 2003; Zacharuk, 1985). Each sensillum has a cuticular component (seta), and one or more sensory neurons; apart from these there are always some structures and/or cavities produced by other associated cells that are also part of the sensilla (Beutel, Friedrich, Yang, & Ge, 2014; Chapman, 1998; Glendinning, 2008). The role of each sensillum depends on its composition, and can be mechano-, chemo-, thermo-, and even hygroreceptors (Altner & Loftus, 1985; Altner & Prillinger, 1980; Giglio, Ferrero, Perrotta, Talarico, & Zetto Brandmayr, 2010; Keil, 1997; Zacharuk & Shields, 1991).

Mechanosensorial sensilla have no pores on its surface (Beutel et al., 2014; Chapman, 1998; Römer, 2003; Zacharuk, 1985). The simplest type is sensillum trichodeum. Chemoreceptor sensilla (i.e., olfactory), have micropores on the surface of its cuticular component (Beutel et al., 2014; Chapman, 1998; Galizia, 2008; Glendinning, 2008; Zacharuk, 1985). However, the type of sensilla by itself does not determine its function, although some of them usually have always the same role. For example, sensillum chaeticum usually acts as mechanoreceptor, but it can sometimes act as contact chemoreceptor (Beutel et al., 2014; Chapman, 1998; Zacharuk, 1985).

Myrmeleontidae, like many other arthropods, usually present various types of cuticular sensilla. Until now, six types of sensilla have been reported for antlion larvae: sensillum trichodeum, sensillum chaeticum, sensillum basiconicum, sensillum campaniformium, digitiform sensillum, and sensillum coeloconicum (Eisenbeis & Wichard, 1987; Lipovšek Delakorda et al., 2009; Devetak et al., 2013).

Sensilla chaetica/trichodea are complex and difficult to interpret because they cover a wide array of different types with subtle variations (Beutel et al., 2014; Chapman, 1998; Zacharuk, 1985), including those commonly referred as "seta" or "bristle." In this work, we have focused on the other types of sensilla, excluding such "bristles."

Among the Myrmeleontidae species whose larvae have been studied using SEM (see Table 1), sensilla (apart from the different forms of "bristles") have been registered for *Distoleon tetragrammicus* (Fabricius, 1798) (Satar et al., 2006), *Neuroleon microstenus* (McLachlan, 1898) (Devetak et al., 2010a; Lipovšek Delakorda et al., 2009), *Myrmecaelurus trigrammus* (Pallas, 1771) (Devetak et al., 2013), *Solter ledereri* Navás, 1912 (Satar, Tusun, & Aykut, 2014), *Gepus gibbosus* Hölzel, 1968 (Satar, Tusun, & Bozdoğan, 2014), *Myrmeleon formicarius* Linnaeus, 1767 (Eisenbeis & Wichard, 1987; Lipovšek Delakorda et al., 2009), *M. yemenicus* Hölzel, 2002 (Devetak et al., 2010b), *Euroleon nostras* (Geoffroy in Fourcroy, 1785) (Lipovšek Delakorda et al., 2009) and *Cueta lineosa* (Rambur 1842) (Tusun, 2020). It is noteworthy that all these papers report about Old World species, and in most of these papers, only a few of the present sensilla are noted.

The work of Devetak et al. (2013) stands out: it elaborates on these sensorial structures in *Myrmecaelurus trigrammus*, also indicating the functions in which each type of sensilla are likely involved. However, we are far from understanding these questions, and further studies are needed to fully assess the role of sensilla in these animals.

Here, the sensilla and other types of tegumentary structures identified using SEM in several larvae of 29 species in 18 genera of Myrmeleontidae, all of them inhabitants of environments with sand, friable stones, dust and/or loose dirt, are described, and their probable or potential functions are specified.

2 | MATERIALS AND METHODS

2.1 | Scanning electron microscopy

2.1.1 | Sample preparation

We use scanning electron microscopy (SEM) at the National Electronic Microscopy Center of the Universidad Complutense de Madrid (CNME-UCM) and at the Electronic Microscopy Laboratory of the Instituto de Biología of UNAM (LME-IBUNAM). The specimens studied were either freshly killed or preserved in 75°–80° alcohol. The live specimens were killed after previously being numbed with ethyl acetate; then they were subjected to an ultrasonic bath for 90 s to eliminate particles adhered to their tegument without damaging or breaking any body structure.

TABLE 1 Synthesis of the previous antlion larvae studies using SEM

Species studied with SEM	Subfamily and tribe	Sensilla cited	Distribution	Reference
Myrmeleon formicarius Linnaeus, 1767	Myrmeleontinae Myrmeleontini	YES	Palearctic (widespread)	Eisenbeis y Wichard, 1987
Distoleon tetragrammicus (Fabricius, 1798)	Nemoleontinae Nemoleontini	YES	Western Palearctic (widespread)	Satar, Suludere, Canbulat, & Özbay, 2006
Myrmeleon bore (Tjeder, 1941) *Myrmeleon inconspicuus* Rambur, 1842	Myrmeleontinae Myrmeleontini Myrmeleontinae Myrmeleontini	NO	Palearctic (widespread) Southern Europe (widespread), northern Africa (widespread), Middle East east to Iran	Nicoli Aldini, 2007
Neuroleon microstenus (McLachlan, 1898) *Myrmeleon formicarius* Linnaeus, 1767 *Euroleon nostras* (Geoffroy in Fourcroy, 1785)	Nemoleontinae Nemoleontini Myrmeleontinae Myrmeleontini Myrmeleontinae Myrmeleontini	YES	Southeastern Europe (widespread), northern Africa (Algeria, Tunisia), Middle East (widespread) Palearctic (widespread) Europe (widespread), northern Africa, Middle East	Lipovšek Delakorda et al., 2009
Megistopus flavicornis (Rossi, 1790) *Gymnocnemia variegata* (Schneider, 1845)	Nemoleontinae Megistopini Nemoleontinae Megistopini	NO	Southern and Central Europe (widespread), northern Africa, Middle East to Iran Southern Europe (widespread), northern Africa (Tunisia, Egypt), Middle East (widespread) east to Turkmenistan	Cesaroni, Nicoli Aldini, and Pantaleoni (2010)
Neuroleon microstenus (McLachlan, 1898)	Nemoleontinae Nemoleontini	YES	Southeastern Europe (widespread), northern Africa (Algeria, Tunisia), Middle East (widespread)	Devetak, Lipovšek, & Pabst, 2010a
Myrmeleon yemenicus Hölzel, 2002	Myrmeleontinae Myrmeleontini	YES	Yemen (Asia)	Devetak, Lipovšek, & Pabst, 2010b
Myrmeleon mariaemathildae Pantaleoni, Cesaroni, & Nicoli Aldini, 2010	Myrmeleontinae Myrmeleontini	NO	Italy (Sardegna), Tunisia	Pantaleoni et al., 2010
Mymecelurus trigrammus (Pallas, 1771)	Myrmeleontinae Myrmecaelurini	YES	Southern Europe (widespread), Middle East (widespread) to Afghanistan	Devetak et al., 2013
Euroleon nostras (Geoffroy in Fourcroy, 1785)	Myrmeleontinae Myrmeleontini	YES	Europe (widespread), northern Africa, Middle East	Devetak, 2014
Solter ledereri Navás, 1912	Myrmeleontinae Gepini	YES	Georgia, Iran, Israel, Lebanon, Syria, Turkey	Satar, Tusun, & Aykut, 2014
Gepus gibbosus Hölzel, 1968	Myrmeleontinae Gepini	YES	Iran, Turkey	Satar, Tusun, & Bozdoğan, 2014
Tricholeon relictus Hölzel y Monserrat, 2002	Dendroleontinae Dendroleontini		South of Spain	Badano, Aspöck, Aspöck, & Cerretti, 2017
Nemoleon notatus (Rambur, 1842)	Nemoleontinae Nemoleontini	NO	Southern Europe (Italy, Spain), northern and middle Africa (widespread), Madagascar	
Deleproctophylla australis (Fabricius, 1787)	Ascalaphinae Ascalaphini		southern Europe (widespread)	
Puer maculatus (Olivier, 1790)	Ascalaphinae Ascalaphini		France, Israel, Spain, northern Africa	
Cueta lineosa (Rambur, 1842)	Myrmeleontinae Nesoleontini	YES	Eastern Europe (Albania, Greece, Italy, western Russia), northern Africa (widespread), Middle East (widespread) east to India	Tusun, 2020

Note: Sensilla cited do not include bristles.

The following SEM protocol was implemented according to Devetak et al. (2010a, 2010b, 2013). The specimens were fixed in 2.5% glutaraldehyde and 4% paraformaldehyde in PBS 0.1 mol/L solution (with 7–7.1 pH) for 24 hr at room temperature. Subsequently, they were washed in an osmium buffer (diluted to 1%) for 90 min and then dehydrated through series of increasing concentrations of ethanol solutions, beginning with 30% alcohol and increasing by 10% the alcohol concentration at each step until a 100% alcohol concentration

TABLE 2 Material studied

Species	Subfamily and tribe	Studied specimens	Collected data	Conservation	Distribution
Tricholeon relictus Hölzel y Monserrat, 2002	Dendroleontinae Dendroleontini	2	Spain: Granada: La Herradura, 8.VII.2013. 2 specimens, F. Acevedo, V. J. Monserrat, D. Badano legs.	Alcohol 70°	Spain (Granada)
Creoleon lugdunensis (Villers, 1789)	Nemoleontinae Nemoleontini	2	Italy: Portici, NA. VI.2011, ex ovo. 1 specimen, E. Labriolo leg. Spain: Madrid: Escorial, La Herrería, 14.6.2011, 1 specimen, F. Acevedo leg.	Alcohol 70°	Southern Europe, northern Africa, Middle East, India
Creoleon aegyptiacus Rambur, 1842	Nemoleontinae Nemoleontini	4	Spain: Almería: Amoladeras, 15.VI.2013, 2 specimens*; 6.VII.2013, 2 specimens#, F. Acevedo, V. J. Monserrat, D. Badano legs.	*Alcohol 70°; # fresh	Southern Europe (widespread), northern and eastern Africa (widespread), Middle East to China (Xinjiang) and Mongolia
Macronemurus appendiculatus (Latreille, 1807)	Nemoleontinae Nemoleontini	1	Italy: Cerdeña, Sassari, Alghero, Capo Caccia, 13.V.2012, 1 specimen, R. A. Pantaleoni, D. Badano legs.	Alcohol 70°	Southern Europe, northern Africa, Middle East
Distoleon annulatus (Klug, 1834)	Nemoleontinae Nemoleontini	2	Spain:Almería, La Torta, San José, 5. VII.2013, 2 specimens, F. Acevedo, V. J. Monserrat, D. Badano legs.	Alcohol 70°	Southern Europe (widespread), northern Africa (widespread), Middle East
Distoleon tetragrammicus (Fabricius, 1798)	Nemoleontinae Nemoleontini	2	France: Gard, Genirac, 29.8.2011, 1 specimen, D. Badano leg. Spain: Barcelona: San Margall, 20.VII.1989, 1 specimen, J. A. Barrientos leg.	Alcohol 70°	Western Palearctic (widespread)
Neuroleon arenarius (Navás, 1904)	Nemoleontinae Nemoleontini	1	Spain: Cádiz: Estación de la Almoraima, 25.V.2012, 1 specimen, F. Acevedo, V. J. Monserrat legs.	Alcohol 70°	Southern Europe (widespread), northern Africa, Middle East
Neuroleon egenus (Navás, 1915)	Nemoleontinae Nemoleontini	4	Spain: Cádiz: Los Alcornocales, 21. VI.2012, 2 specimens, F. Acevedo, V. J. Monserrat legs.; Ciudad Real: Navas de Estena, P.N. Cabañeros, 8.VI.2012, 2 specimens, F. Acevedo leg.	Alcohol 70°	Southern Europe (widespread), northern Africa, Middle East
Neuroleon nemausiensis (Borkhausen, 1791)	Nemoleontinae Nemoleontini	2	Italy: Cerdeña, Sassari:Alghero, Capo Caccia, 14.IX.2010, 1 specimen, D. Badano leg. Spain: Granada: La Herradura, 9.VII.2013, 1 specimen, F. Acevedo, V. J. Monserrat, D. Badano legs.	Alcohol 70°	Southern Europe, northern Africa, Middle East
Neuroleon ocreatus (Navás, 1904)	Nemoleontinae Nemoleontini	3	Spain: Alicante: El Pinet, 18.VII.2013, 2 specimens, F. Acevedo leg.	Fresh	France, Italy, Spain
Megistopus flavicornis (Rossi, 1790)	Nemoleontinae Megistopini	3	Spain: Ciudad Real: Boquerón del Estena, P. N. Cabañeros, 29.VII.2014, 2 specimens* +1specimen#, F. Acevedo leg.	*Alcohol 70°; # fresh	Southern and Central Europe (widespread), northern Africa, Middle East to Iran
Gymnocnemia variegata (Schneider, 1845)	Nemoleontinae Megistopini	4	Spain: Granada: Cerro Gordo, 21. IV.2011, 2 specimens*, F. Acevedo y V. J. Monserrat legs.; Huesca: Parzán, 16. VIII.1978, 1 specimen*, V. J. Monserrat leg.; Cádiz: Los Alcornocales, 7. IV.2015, 1 specimen#, F. Acevedo leg.	*Alcohol 70°; # fresh	Southern Europe (widespread), northern Africa (Tunisia, Egypt), Middle East (widespread) east to Turkmenistan
Purenleon paralellus (Schneider, 1845)	Nemoleontinae Glenurini	3	Mexico: Chiapas: La Encrucijada, 7. IV.2017, 3 specimens, F. Acevedo, P. Abad, R. J. Cancino legs.	Fresh	Mexico, Honduras, Costa Rica, Panama, Colombia
Purenleon sp.	Nemoleontinae Glenurini	2	Mexico: Nuevo León: Cerro Potosí, 13. X.2017, 2 specimens, F. Acevedo, R. Lopez, A. Contreras-Ramos legs.	Alcohol 70°	Mexico

TABLE 2 (Continued)

Species	Subfamily and tribe	Studied specimens	Collected data	Conservation	Distribution
Eremoleon vitreus (Navás, 1914)	Nemoleontinae Glenurini	2	Mexico: Puebla: Zapotitlán de las Salinas, 24.III.2017, 2 specimens, F. Acevedo, P. Abad, R. López legs.	Fresh	Mexico
Myrmecaelurus trigrammus (Pallas, 1771)	Myrmeleontinae Myrmecaelurini	4	Spain: Almería: Playa de los Genoveses, San José, 16.VI.2013, 2 specimens*, F. Acevedo leg.; 6.VII.2013, 2 specimens, F. Acevedo, V. J. Monserrat, D. Badano legs.#	*Alcohol 70°; # fresh	Southern Europe (widespread), Middle East (widespread) to Afghanistan
Solter liber Navás, 1912	Myrmeleontinae Gepini	1	Spain: Almería: Rambla Oasis, Tabernas, 15.VI.2013, 1 specimen, F. Acevedo leg.	Alcohol 70°	Southwestern Europe (Portugal, Spain), northern Africa (widespread), Middle East (Turkey)
Acanthaclisis occitanica (Villers, 1789)	Myrmeleontinae Acanthaclisini	4	Spain: Almería: Retamar, 12.VII.2012, 2 specimens, F. Acevedo leg.; Rambla Torregarcía, 15.VI.2013, 1 specimen, F. Acevedo leg.; San José, Playa de los Genoveses, 6.VII.2013, 1 specimen, F. Acevedo, V. J. Monserrat, D. Badano legs.	Alcohol 70°	Western Palearctic (widespread) east to India
Synclisis baetica (Rambur, 1842)	Myrmeleontinae Acanthaclisini	4	Spain: Murcia: Playa de Calblanque, 20.IX.1995, 1 specimen, V. J. Monserrat leg.; Almería, Rambla Morales, 14.IX.2014, 1 specimen, F. Acevedo leg.; Rodalquilar, El Playazo, 12.VII.2014, 2 specimens, F. Acevedo leg.	Alcohol 70°	Southern Europe, northern Africa, Middle East
Vella fallax (Rambur, 1842)	Myrmeleontinae Acanthaclisini	2	Mexico: Yucatán: Sisal; 2 specimens; F. Acevedo, R. López García, P. Abad legs.	Fresh	Southern United States (widespread), Mexico (widespread) south to Argentina, West Indies (Cayman Islands, Cuba, Haiti, Puerto Rico)
Myrmeleon formicarius Linnaeus, 1767	Myrmeleontinae Myrmeleontini	4	Spain: Madrid: Abantos, 4.VII.2012, 2 specimens, F. Acevedo leg.; 29.6.2013, 2 specimens, F. Acevedo leg.	Alcohol 70°	Palearctic (widespread)
Myrmeleon gerlindae Hölzel, 1974	Myrmeleontinae Myrmeleontini	2	Spain: Huelva: Arroyo Julianejo, 24.V.2012, 1 specimen, F. Acevedo, V. J. Monserrat legs.; Granada: La Herradura, Cerro Gordo, 2.IX.2000, 1 specimen, V. J. Monserrat leg.	Alcohol 70°	France, Italy, Morocco, Spain
Myrmeleon inconspicuus Rambur, 1842	Myrmeleontinae Myrmeleontini	4	Spain: Ciudad Real: El Chorro, P. N. Cabañeros, 20.VI.2014, 2 specimens#, F. Acevedo leg.; Huelva: Punta Umbría, 24.V.2012, 2 specimens*, F. Acevedo, V. J. Monserrat legs.	*Alcohol 70°; # fresh	Southern Europe (widespread), northern Africa (widespread), Middle East east to Iran
Myrmeleon hyalinus Olivier, 1811	Myrmeleontinae Myrmeleontini	6	Spain: Almería: Rambla Torregarcía, 14.VI.2012, 2 specimens, F. Acevedo leg.; Amoladeras, 11.VII.2014, 2 specimens, F. Acevedo leg.; Rodalquilar, El Playazo, 11.VII.2014, 2 specimens, F. Acevedo leg.	Alcohol 70°	Southern Europe (widespread), northern Africa (widespread), Middle East (widespread) east to western India, Atlantic islands (Spain [Canary Islands], Cape Verde)
Myrmeleon almoharadum Badano, Acevedo,	Myrmeleontinae Myrmeleontini	3	Spain: Cádiz: Las Cañillas, 25.V.2012, 2 specimens, F. Acevedo, V. J. Monserrat legs.; Cádiz: Bolonia, 24.V.2012, 1	Alcohol 70°	Spain and Tunisia

(Continues)

TABLE 2 (Continued)

Species	Subfamily and tribe	Studied specimens	Collected data	Conservation	Distribution
Pantaleoni y Monserrat, 2016			specimen, F. Acevedo, V. J. Monserrat legs.		
Myrmeleon sp.	Myrmeleontinae Myrmeleontini	2	México; Puebla: Zapotitlán de las Salinas, R. B. Tehuacán-Ciucatlán; 2 specimens; F. Acevedo, R. López García legs..	Alcohol 70°	Mexico
Euroleon nostras (Geoffroy en Fourcroy, 1785)	Myrmeleontinae Myrmeleontini	3	Spain: Guadalajara: Zaorejas, 24. VIII.2013, 3 specimens, F. Acevedo leg.	Alcohol 70°	Europe (widespread), northern Africa, Middle East
Scotoleon quadripunctatus (Currie, 1898)	Myrmeleontinae Brachynemurini	2	Mexico: Tamaulipas, La Pesca; 2 specimens; F. Acevedo, R. J. Cancino legs.	Fresh	Southwestern United Sates (AZ, CA, NV, TX), northwestern Mexico (BCS, SON)
Brachynemurus hubbardii Currie, 1898	Myrmeleontinae Brachynemurini	2	Mexico: Tamaulipas, La Pesca; 2 specimens; F. Acevedo, R. J. Cancino legs.	Fresh	Southwestern United States (widespread), Mexico (widespread)

was reached (in total, 15 steps). At each step, the specimens underwent two 1-hr immersions, except when in 70% alcohol they were left overnight. After leaving the material in absolute alcohol, they were stored for at least 24 hr and then taken to the SEM facility, to apply critical point drying. Then, the specimens were mounted on metallic plates with adhesive tape and coated with gold. After this, samples were studied and photographed with the CMNE's JEOL JSM 6400 scanning electronic microscope at 15–20 kV, and a HITACHI SU1510 at LME-IBUNAM. The recorded scale and measurements were taken directly from the microscope's software. The specimens preserved in 70% alcohol received the same treatment, but they were not fixed in glutaraldehyde and paraformaldehyde.

2.1.2 | Material studied

The study covers 29 species of 18 genera belonging to three of the four subfamilies recognized by Machado et al. (2019): Myrmeleontinae, Dendroleontinae and Nemoleontinae. All the species are totally or at least partially psammophilous.

The species, tribes (sensu Machado et al., 2019), number of specimens, collecting data, as well as the medium in which the specimens were placed before fixation for SEM study appear in Table 2. In the "conservation" column, an asterisk (*) indicates when alcohol was the usual preservative for the specimens and a number sign (#) when they were freshly killed. The distribution of each species is also provided (Table 2). The European specimens were studied at CNME and the American ones at LME-IBUNAM.

2.1.3 | Structures studied

The study focused mainly on sensilla and other cuticular structures (excluding "bristles"). We follow the nomenclature by Zacharuk (1985) and Lipovšek Delakorda et al. (2009). The main regions of the body are named as in Badano and Pantaleoni (2014).

The sensilla and other types of cuticular structures observed are described and illustrated. Their suggested function is inferred after Zacharuk and Shields (1991), Römer (2003) and Devetak et al. (2013).

3 | RESULTS

The types of sensilla and other tegumentary structures observed and their probable or potential functions are presented below. The information given is shared by all the studied species, and no differences between clades or species were found (unless otherwise specified). The part of the larval body where they are found, as well as their number and shape, are indicated.

3.1 | Sensilla

A total of six different kinds of sensilla have been observed in the antlion larvae: coeloconica, basiconica, campaniformia, trichodea (two types), and placodea (Figure 1).

- Sensilla coeloconica: structures consisting of a cavity with a short seta inside, whose tip is often visible through an orifice in the cuticle (Figure 1, red circle). Function: thermo-, hygro-, or chemoreceptor.
- Sensilla basiconica: in the larvae under study, these structures consist of claviform or conical setae (Figure 1, green circle). Usually, they are grouped in variable number; rarely is one found isolated. Function: olfactory, chemoreceptor.
- Sensilla campaniformia: cuticular depression with a boss in its bottom, which is often not visible. For this reason, they are normally identified as cuticular orifices, though in the studied larvae the boss

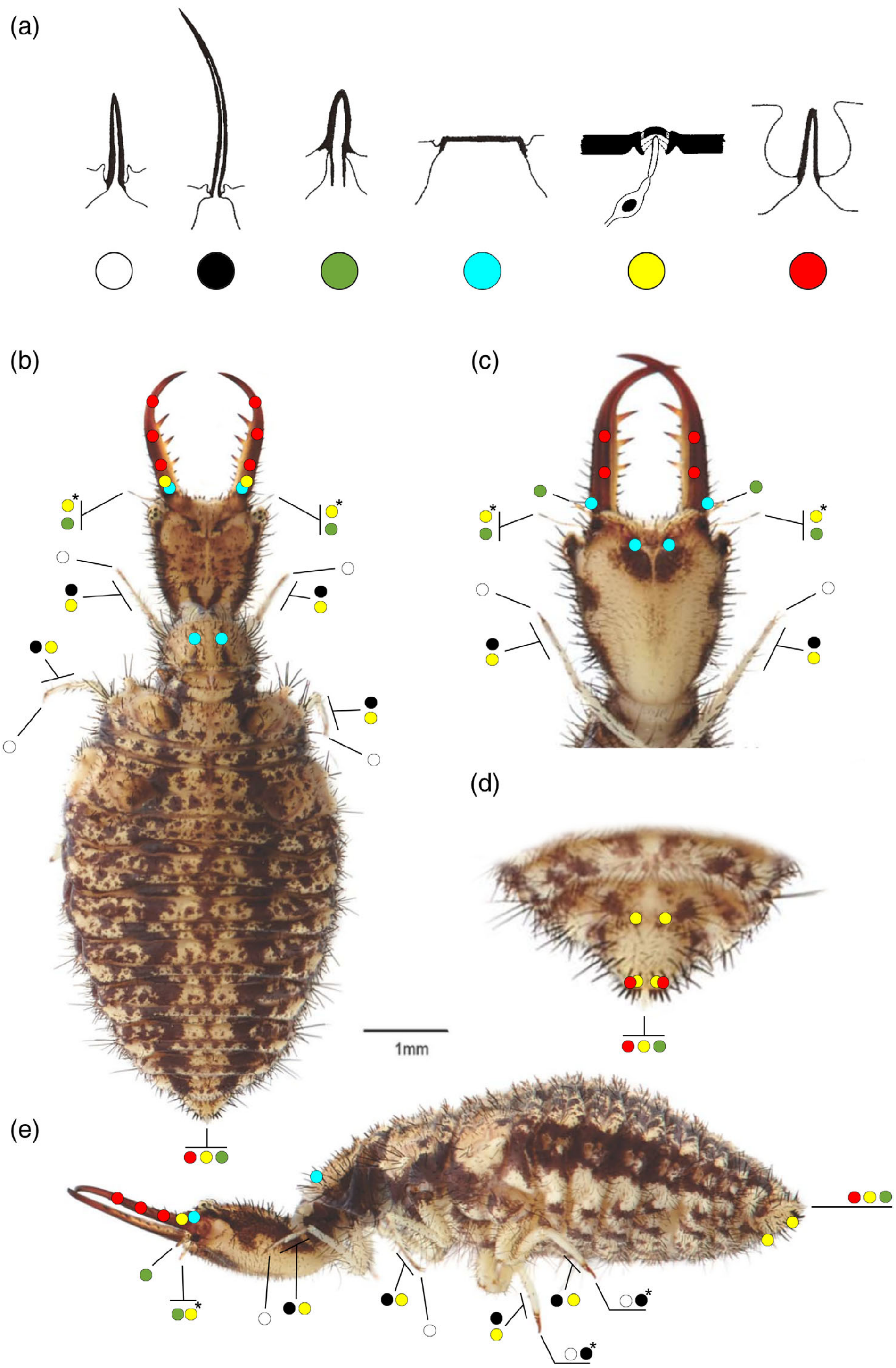

FIGURE 1 Types of sensilla and position in larval body of Myrmeleontidae. (a) kinds of sensilla adapted from Zacharuk (1985) and Keil (1997): sensillum tricoideum (type I, white circle; type II, black circle); sensillum basiconicum (green circle); sensillum placodeum (blue circle); sensillum campaniformium (yellow circle); sensillum coeloconicum (red circle). (b–e) Habitus of a Myrmeleontidae larva; (b) dorsal view; (c) head capsule, ventral view; (d) last abdominal sternites; (e) lateral view. Sensilla mapped and coded following the colors of (a)

is sometimes observed slightly protruding on the surface (Figure 1, yellow circle). Function: detecting tactile and/or vibrational stimuli/mechanoreceptor.

- Sensilla trichodea: hair- or spine-like, erect seta. There is some confusion within "trichoid" type sensilla, because distinction between sensilla chaetica and sensilla trichodea is based only on the width of the insertion area, being very similar in their morphology. Therefore, this type of sensorial organ is treated as "sensilla trichodea" sensu *lato* (Figure 1, white and black circles). A distinction is made, however, between type I sensilla trichodea, which are short and relatively stout, usually present on legs and tarsal claws; type II sensilla trichodea are slenderer and more elongate. Function: mechanoreceptor and contact chemoreceptor.
- Sensilla placodea: scale or plate-shaped structure situated slightly above the cuticular surface of the larvae (Figure 1a, blue circle). Function: chemoreceptor.

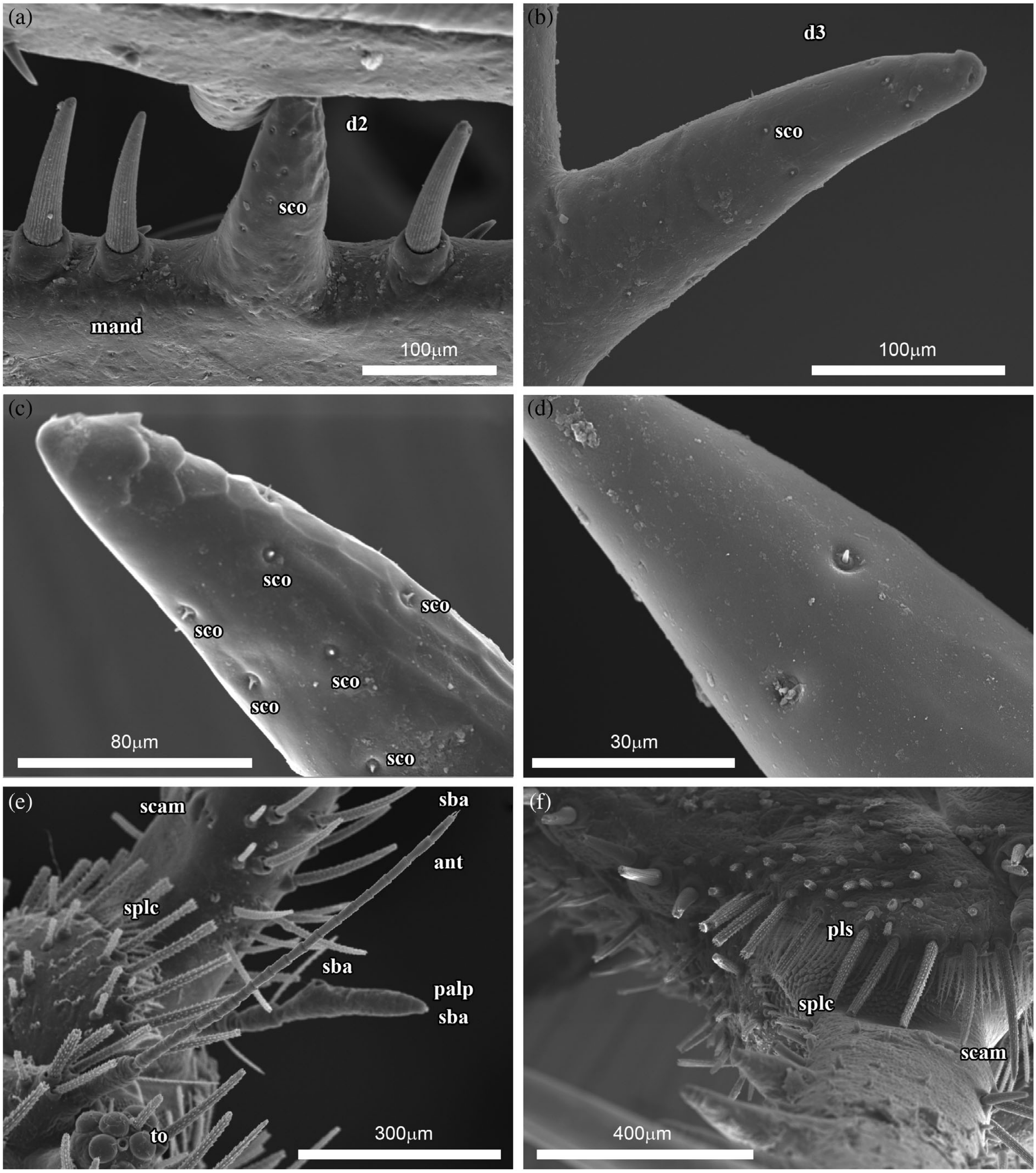

FIGURE 2 Scanning electron micrographs of third instar larvae of different antlion species. (a) Detail of mandibles of *Myrmecaelurus trigrammus*, ventral view; (b) third mandibular tooth of *Tricholeon relictus*, dorsal view; (c) first mandibular tooth of *Distoleon tetragrammicus*, latero-dorsal view; (d) second mandibular tooth of *Euroleon nostras*, dorsal view; (e) region of insertion of mandibles, antenna and ocular tubercle of *Tricholeon relictus*, latero-dorsal view; (f) region of insertion of mandibles of *Distoleon tetragrammicus*, anterior-dorsal view. ant, antenna; d2, d3, mandibular teeth 2 and 3; mand, mandibles; palp, labial palpus; pls, plumose hairs; sba, sensilla basiconica; scam, sensilla campaniformia; sco, sensilla coeloconica; splc, sensilla placodea; to, ocular tubercle

3.2 | Other tegumentary structures

Apart from sensilla there are two types of tegumentary structures which could play a significant role in the adaptation to psammophilous lifestyles:

- Porous surfaces: a portion of cuticle with scattered pores (Figures 3a,c–f, 4a–c), likely chemoreceptor.
- Dentate surfaces: several aligned denticles (Figure 5b–d), probably associated to mechanic attachment of certain mouthparts.

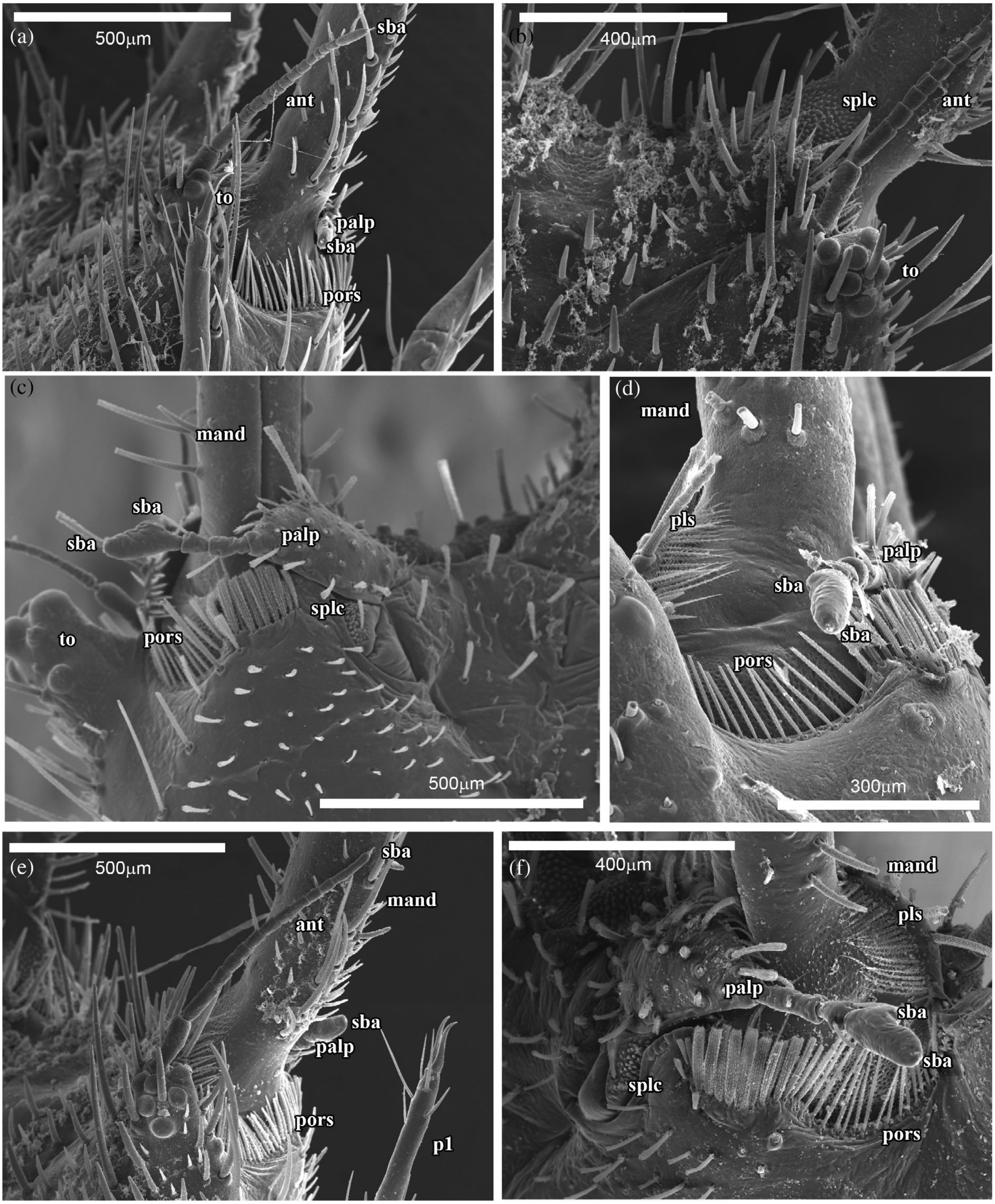

FIGURE 3 Scanning electron micrographs of third instar larvae of different antlion species. (a) Region of insertion of mandibles, antenna and ocular tubercle of *Euroleon nostras*, lateral view; (b) region of insertion of mandibles, antenna and ocular tubercle of *Myrmeleon hyalinus*, lateral-dorsal view; (c) anterior region of head capsule, clipeo-labrum, insertion of mandibles and maxilla and labial palpus de *Gymnocnemia variegata*, ventral view; (d) region of insertion of mandibles and labial palpus de *Creoleon aegyptiacus*, lateral view; (e) region of insertion of mandibles, antenna and ocular tubercle of *Myrmeleon gerlindae*, lateral-dorsal view; (f) anterior region of head capsule, and region of insertion of mandibles and maxilla, and labial palpus of *Megistopus flavicornis*, lateral-ventral view. ant, antena; mand, mandibles; p1, prothoracic leg; palp, labial palpus; pors, porous region; pls, plumose hairs; sba, sensilla basiconica; splc, sensilla placodea; to, tubercle

3.3 | Location of sensilla and other tegumentary structures on larvae

The sensilla and sensory structures that were observed in this study are detailed below according to the body region on which they occur (see Figure 1).

3.3.1 | Mandibles

The entire mandibular surface and teeth are densely covered with sensilla coeloconica, and their distribution is roughly uniform (Figures 2a–d, 5b). Toward the basal area of the mandibles, a few sensilla campaniformia could be observed (Figure 2e–f). Sensilla coeloconica were also observed on the surface of the maxillae (Figure 5c,d).

On the dorsal area of the mandibular insertion, there are very thick plumose setae surrounding a granular surface (Figures 2e–f, 3a, b). This granular surface appears to be composed of sensilla placodea (Figures 2e,f, 3b); these sensilla also appear on the lateral inferior mandibular area (Figures 3f, 4a). These plumose setae are much stouter than those on the rest of the larval body and they are similar in all the species studied in this work.

On the other hand, these thick plumose setae also appear surrounding a porous surface located on the external part of the mandibular insertion. The pores in this area are large (Figures 3d–f, 4a–c) and, given its location and the type of setae that surrounds it, are considered to fulfill a sensory function, probably as chemoreceptors. Additionally, the plumose setae that surrounds this area seems to contribute to the protection of this structure.

Likewise, there are sensilla coeloconica on the inner surface of the food canal, located between mandibles and maxillae (Figure 5b, e–f). These sensilla have been found only in specimens of *Myrmeleon inconspicuus* and *Scotoleon quadripunctatus* specially prepared for the study of these mouthparts.

The dentate surfaces are located on the maxillae (Figure 5b–d), on the contact areas with the mandibles. These denticles in the maxilla corresponds with a series of parallel notches in the surface of the mandible (Figure 5b–d) in direct contact with the maxilla. This mechanism anchors both structures, closing the food canal (Figure 5a–d).

3.3.2 | Cephalic capsule

Sensilla placodea occur on the ventral region of the head, close to the mandibles; on the mentum and the cardo (Figure 3c,f). A pattern of three sensilla basiconica has been observed on the tip the antennae (Figure 4d–f); with all the studied species sharing the same pattern (Figures 2e, 3a,e, 4a, d–f). In *Synclisis baetica*, there is a sensillum campaniformium surrounding the area where sensilla basiconica are situated, but we have not found it in any of the other species (Figure 4f).

On the labial palpi there are numerous grouped sensilla basiconica in the last palmomere, arranged in two groups: one group on the middle or subterminal area and another on the apex (Figures 2e, 3a,c–f, 4a, 6a–f). The number of sensilla is high in both groups. The position of the first group varies minimally according to the species, and these sensilla often appear in a crater-shaped cuticular depression (Figures 2e, 3a, c–f, 4a, 6a,b). The second group on the apex of the palpi do not appear in cuticular depressions (Figure 6c, e,f) in the studied species, except in *Solter liber*, where these sensilla are also enclosed in a crater-like depression (Figure 6d).

3.3.3 | Thorax and legs

On the thorax, the surface of the pronotum presents a granular texture, as has been described in previous studies (Devetak et al., 2010a, 2010b; Satar et al., 2006; Satar, Tusun, & Aykut, 2014; Tusun, 2020). We consider that they could in fact be sensilla placodea: all the species studied using SEM possess this type of texture in the same region (Figure 7a,b).

Between the two tarsal claws of each pair of legs, there are two type I sensilla trichodea (Figure 7c–f, 8a). The size of these sensilla, situated between the tarsal claws, is similar in all species, except in *Tricholeon relictus* where one of them is much longer in the metathoracic pair of legs; to date, this has never been found before in this region in studies on these larvae (Figure 7d). Until now, they had been considered as type II sensilla trichodea.

Additionally, several type II sensilla trichodea have been observed close to the claws of all legs in nearly all species, and some sensilla campaniformia have been observed in areas close to the distal end of the legs (Figures 7c–e, 8a).

3.3.4 | Abdomen

In species that possess odontoid processes on abdominal sternite VIII, there are sensilla campaniformia on their apex (Figure 8b,c). In the ventral region of abdominal sternite IX and on the rastra some sensilla coeloconica and sensilla campaniformia have also been found (Figures 8b, d–f, 9a).

Some specimens, when prepared for SEM, presented an everted X abdominal segment, thus making its observation possible (Figures 8g, 9a–f). In this region, there are various types of sensilla. The sensilla coeloconica are the most frequent, with several of them regularly spaced throughout the length of this segment (Figures 8g, 9c–e) and presenting a longer seta than those found on the mandibular region and on other areas of the body (Figure 9e). In this region, isolated sensilla basiconica have also been observed in *Macronemurus appendiculatus* and *Synclisis baetica* (Figure 9e–f). Lastly, sensilla campaniformia are present (most of them situated subterminally) in smaller number than the sensilla basiconica (Figure 9c,d,f).

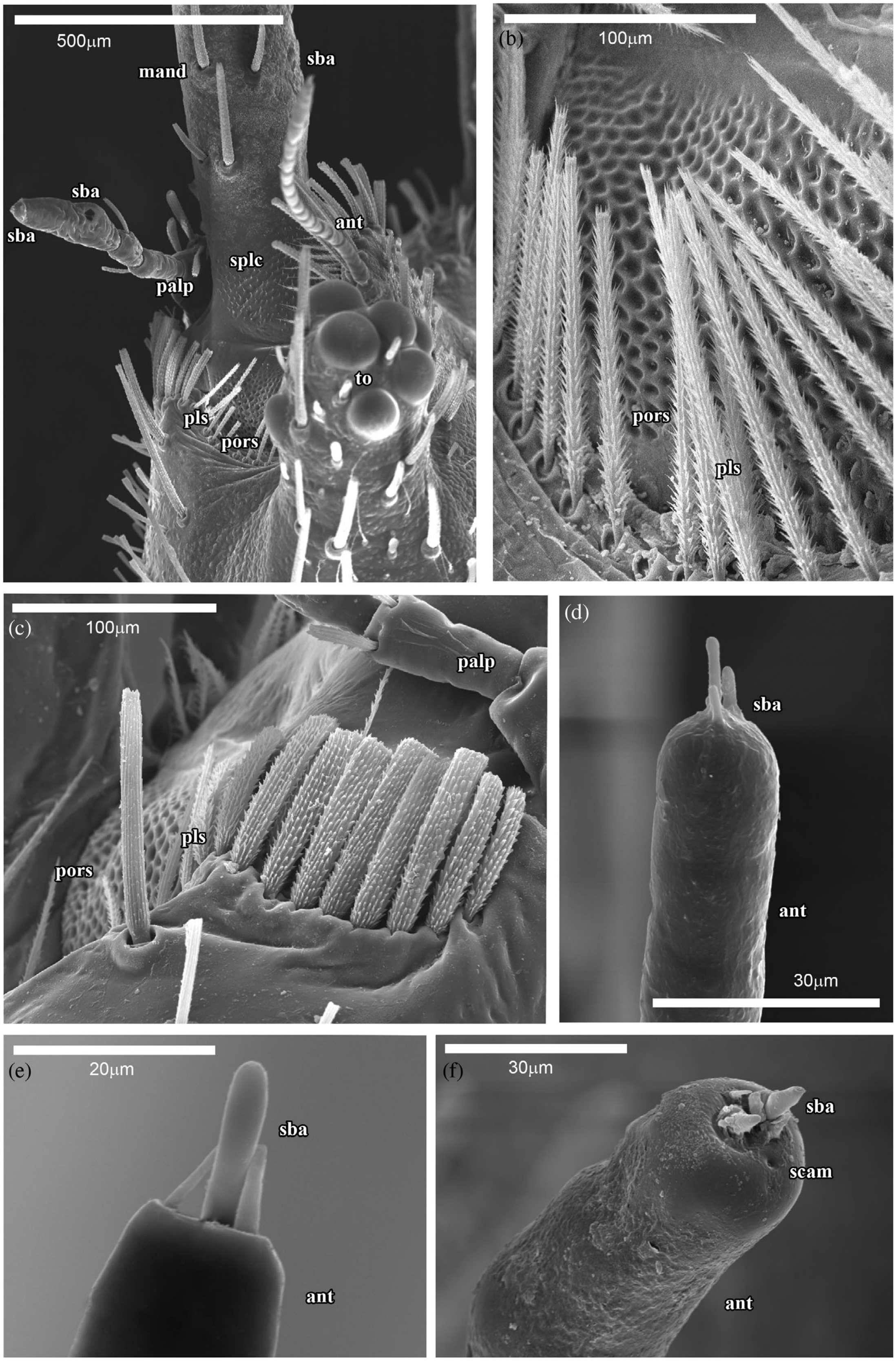

FIGURE 4 Scanning electron micrographs of third instar larvae of different antlion species. (a) Region of insertion of mandibles, antenna and ocular tubercle of *Megistopus flavicornis*, lateral view; (b) detail of porous texture situated on lateral region of mandibles insertion of *Eremoleon vitreus*, lateral view; (c) detail of porous texture situated on lateral region of mandibles insertion of *Neuroleon ocreatus*, latero-ventral view; (d) apex of antenna of *Neuroleon ocreatus*; (e) apex of antenna of *Myrmecaelurus trigrammus*; F: apex of antenna of *Synclisis baetica*. ant, antena; mand, mandibles; palp, labial palpus; pls, plumose hairs; pors, porous texture; sba, sensilla basiconica; scam, sensilla campaniformia; splc, sensilla placodea; to, ocular tubercle

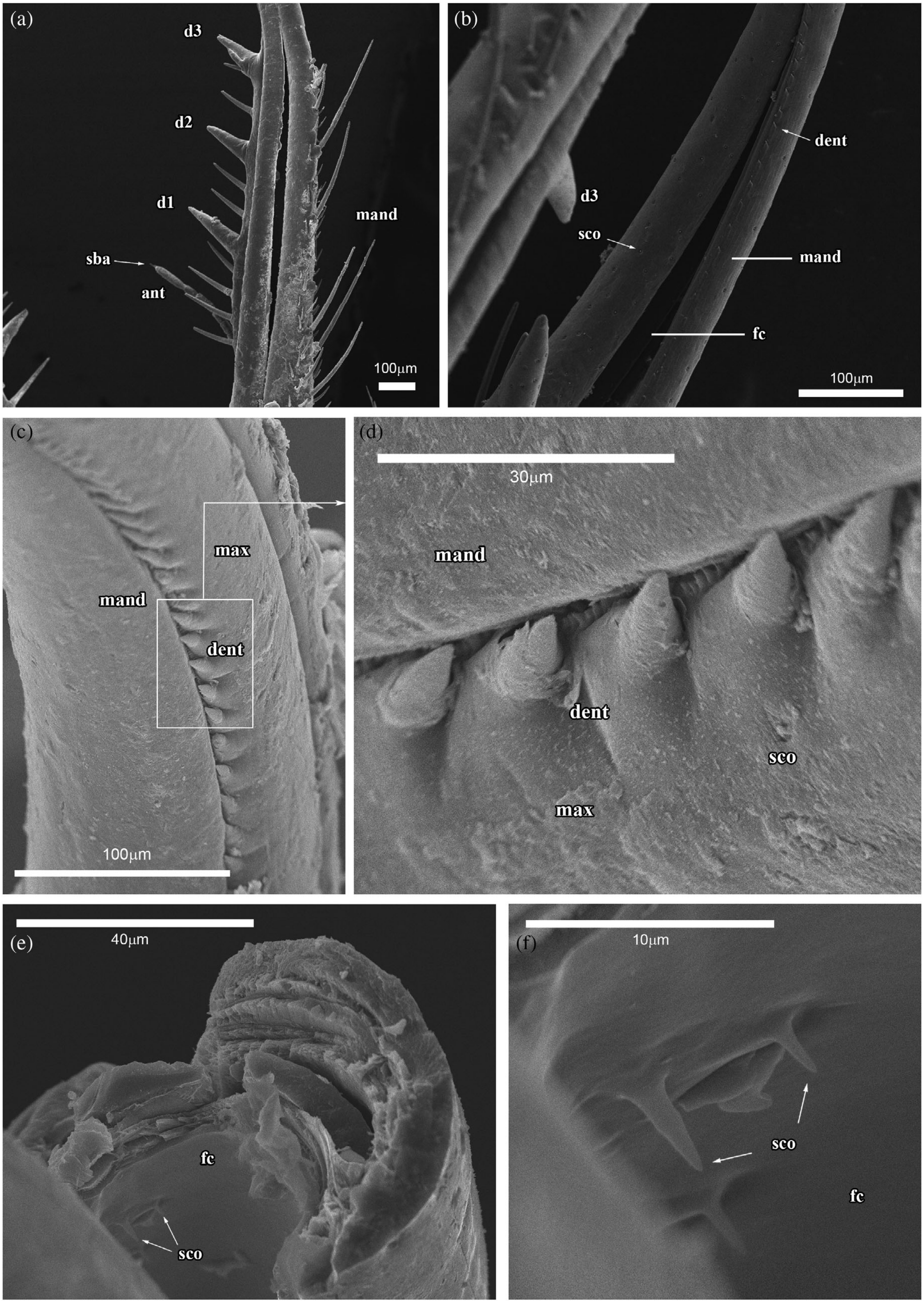

FIGURE 5 Scanning electron micrographs of third instar larvae of different antlion species. (a) *Myrmeleon inconspicuus*, detail of mandible without the maxilla, ventral view; (b) *Myrmeleon hyalinus*, detail of mandible without the maxilla, lateral view; (c) *Vella fallax*, dentate surface on mandible and maxilla, lateral view; (d) *Vella fallax*, *ditto*, lateral view; (e) *Scotoleon quadripunctatus*, inner of food canal; (f) *Scotoleon quadripunctatus*, detail of inner of food canal. ant, antenna; d1, d2, d3, mandibular teeth; dent, dentate surface; food can, food canal; mand, mandible; max, maxilla; sba, sensilla basiconica; sco, sensilla coeloconica

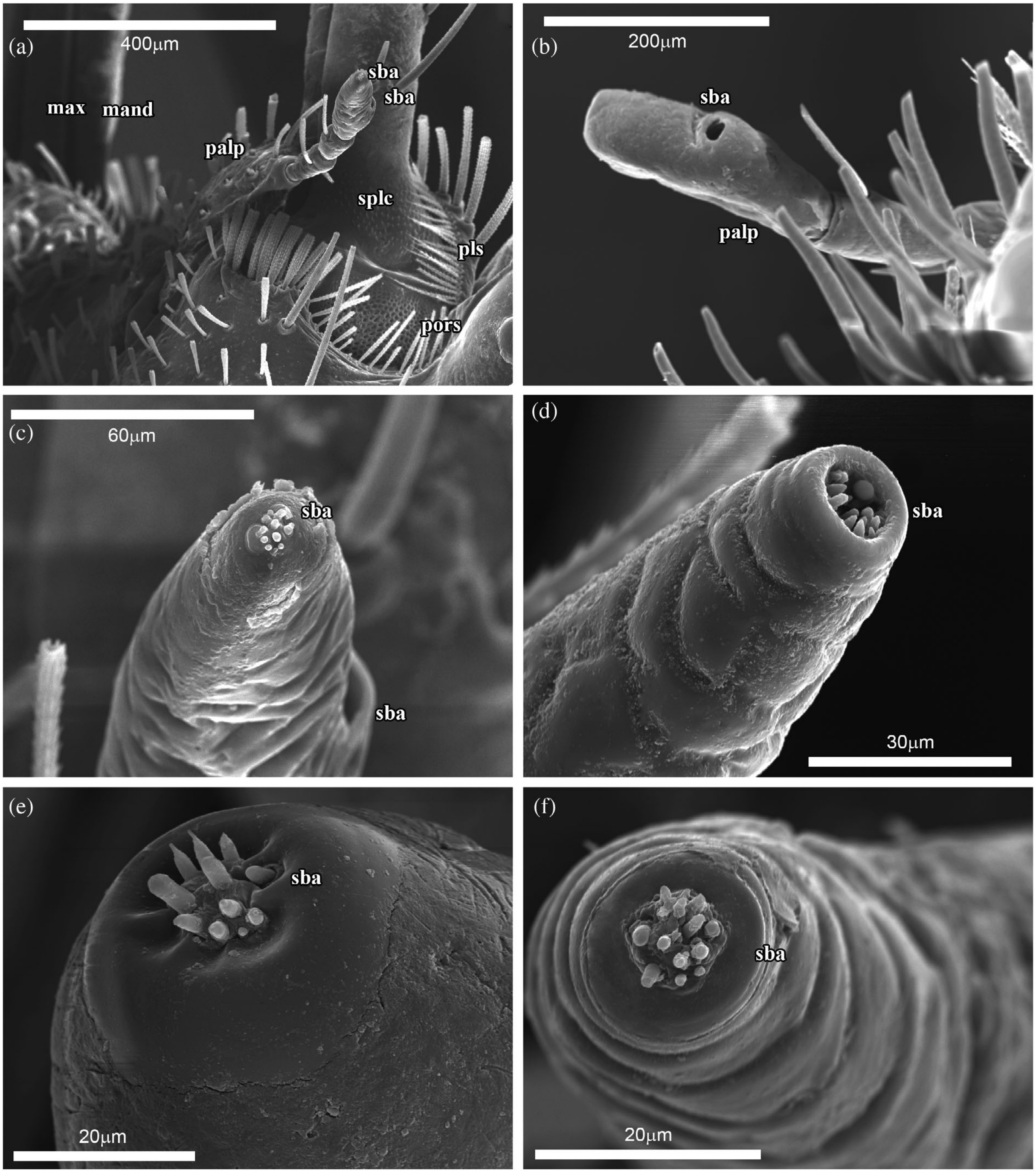

FIGURE 6 Scanning electron micrographs of third instar larvae of different antlion species. (a) Anterior region of head capsule, clipeo-labrum, insertion of mandibles and maxilla, and labial palpus of *Megistopus flavicornis*, latero-ventral view; (b) last two palpomeres of labial palpus of *Acanthaclisis occitanica*, lateral-dorsal view; (c) apex of labial palpus of *Megistopus flavicornis*; (d) apex of labial palpus of *Solter liber*; (e) apex of labial palpus of *Acanthaclisis occitanica*; (f) apex of labial palpus of *Tricholeon relictus*. mand, mandibles; max, maxila; palp, labial palpus; pors, porous texture; pls, plumose hairs; sba, sensilla basiconica; splc, sensilla placodea

4 | DISCUSSION

This is the first comparative study of tegumentary sensory structures in neuropteran species using scanning electron microscopy, although Lipovšek Delakorda et al. (2009) already comment on the sensilla of the larvae of *Neuroleon microstenus*, *Myrmeleon formicarius*, and *Euroleon nostras*. This is also the first study using SEM in which New World species have been included.

The sensilla identified in this study exist in many other insects studied in their larval and adult phases; those sensilla, however, may differ in size and shape (e.g., Keil, 1997; Pérez-González & Zaballos, 2013; Tormos et al., 2013; Zacharuk, 1985; Zacharuk & Shields, 1991).

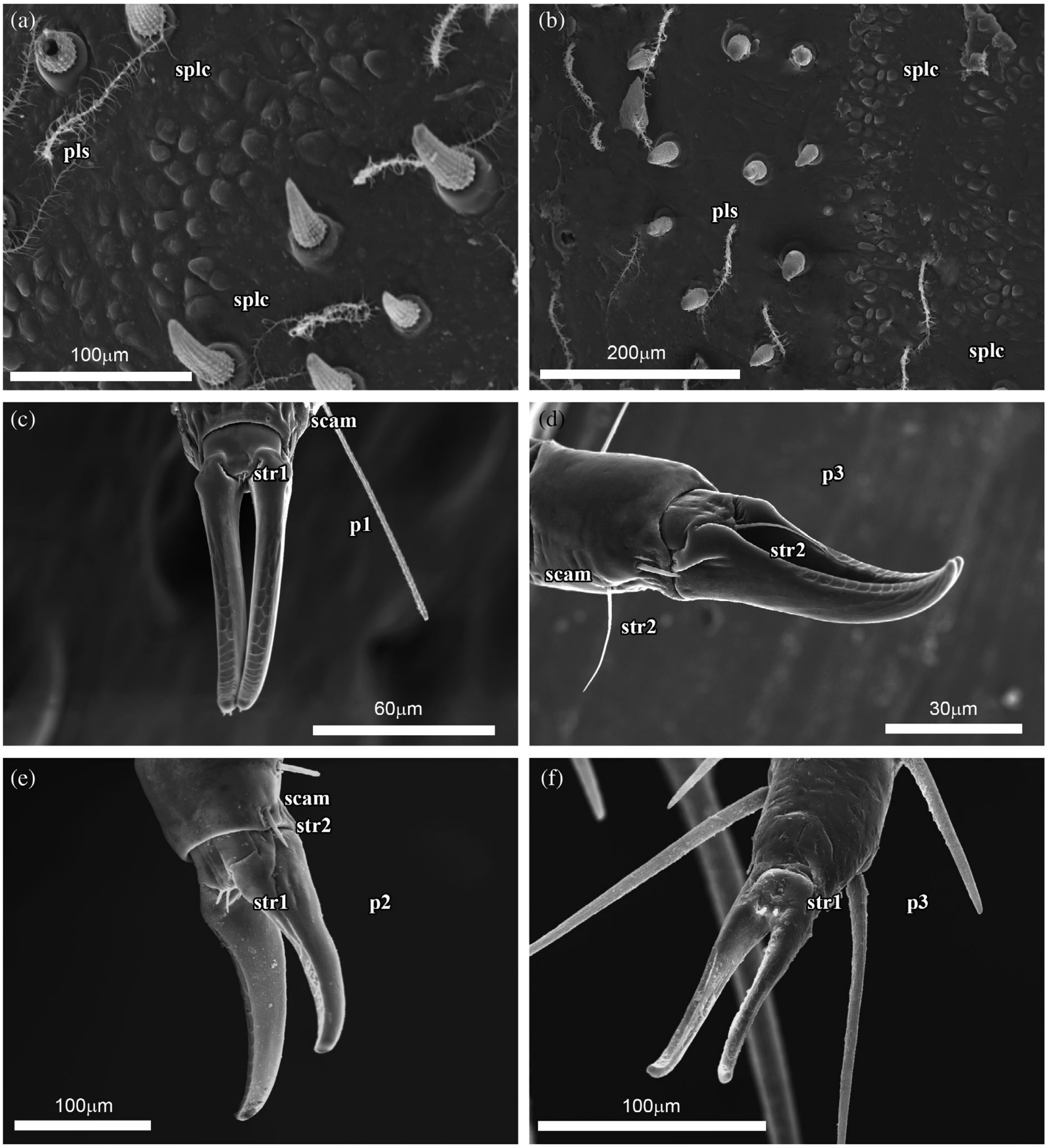

FIGURE 7 Scanning electron micrographs of third instar larvae of different antlion species. (a) Detail of pronotum of *Myrmecaelurus trigrammus*, dorsal view; (b) detail of pronotum of *Acanthaclisis occitanica*, dorsal view; (c) tarsal claws of prothoracic leg of *Solter liber*, ventral view; (d) tarsal claws of metathoracic leg of *Tricholeon relictus*, lateral-ventral view; (e) tarsal claws of mesothoracic leg of *Neuroleon egenus*, lateral view; (f) tarsal claws of metathoracic leg of *Myrmeleon gerlindae*, ventral view. p1, prothoracic leg; p2, mesothoracic leg; p3, metathoracic leg; pls, plumose hairs; scam, sensilla campaniformia; splc, sensilla placodea; str1, type I sensilla trichodea; str2, type II sensilla trichodea

The sensilla, as well as the other cuticular sensory structures observed in Myrmeleontidae larvae, are constant in shape and location on the body surface of the different species; this pattern may be partially inferred from previous studies (Eisenbeis & Wichard, 1987; Devetak et al., 2010a, 2010b, 2013; Lipovšek Delakorda et al., 2009; Satar et al., 2006, 2014, b; Tusun, 2020). Most of the studied sensilla are also observed on the larvae and adults of the order Neuroptera (e.g., Devetak, Pabst, & Lipovšek Delakorda, 2004; Minter, 1992; Suludere, Satar, Candan, & Canbulat, 2006; Vshivkova & Makarkin, 2010; Zimmermann, Klepal, & Aspöck, 2009).

The sensilla coeloconica of the mandibles, the sensilla basiconica on the antennae and labial palpi (despite that the group of subterminal sensilla had only been noted for *M. trigrammus* in Devetak et al., 2013), and the sensilla trichodea between the tarsal claws had

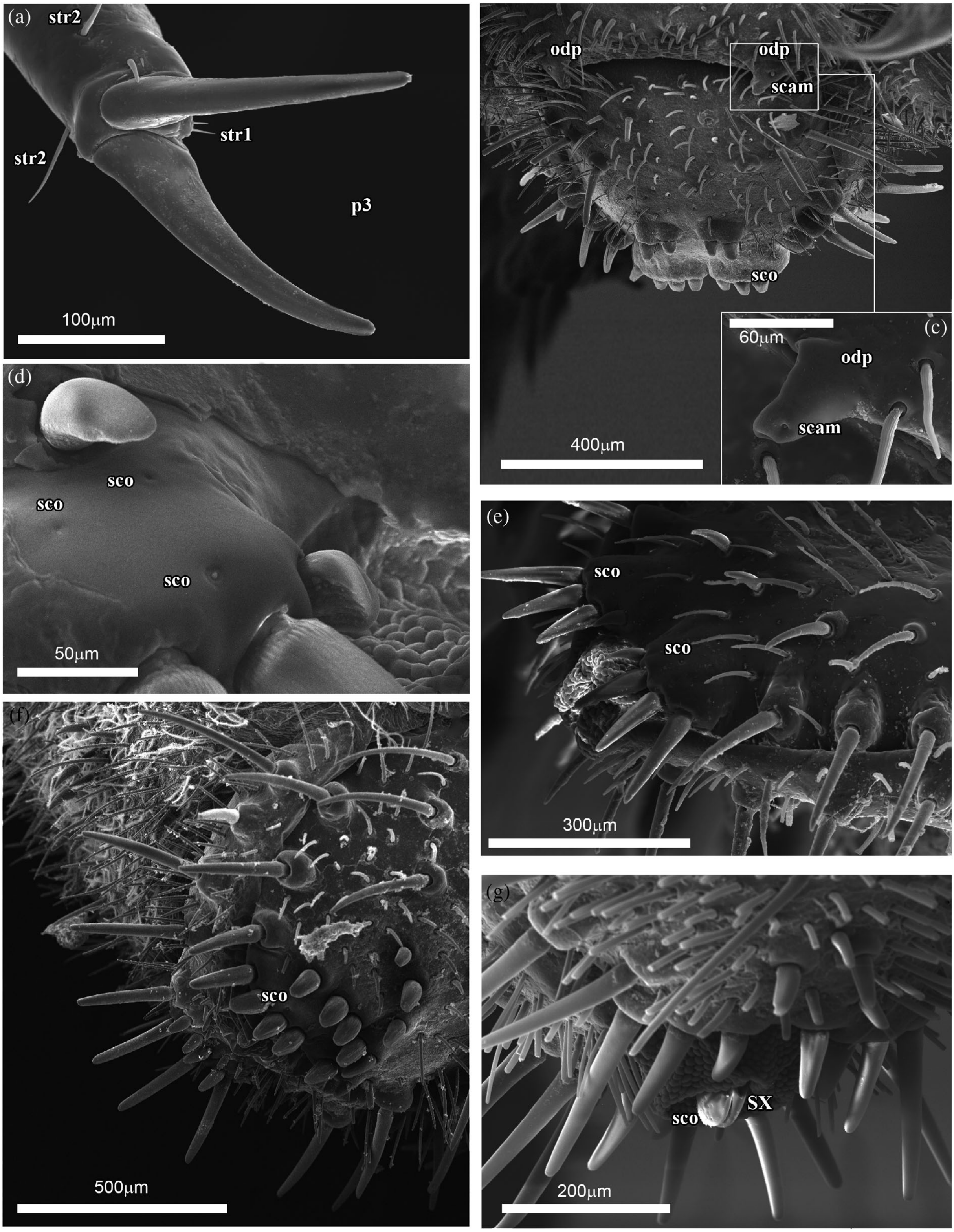

FIGURE 8 Scanning electron micrographs of third instar larvae of different antlion species. (a) Tarsal claws of metathoracic leg of *Neuroleon arenarius*, ventral view; (b) last abdominal segments of *Myrmeleon formicarius*, ventral view; (c) detail of odontoid process of *Neuroleon egenus*, ventral view; (d) detail of rastra in the IX sternite of *Brachynemurus hubbardii*, ventral view; (e) apex of abdomen of *Megistopus flavicornis*, lateral-ventral view; (f) apex of abdomen of *Myrmeleon inconspicuus*, lateral-ventral view; (g) apex of abdomen of *Synclisis baetica*, ventral view. odp, odontoid process; p3, metathoracic leg; scam, campaniform sensilum; sco, sensilla coeloconicum; str1, type I sensilla trichodea; str2, type II sensilla trichodea; SX, abdominal segment X

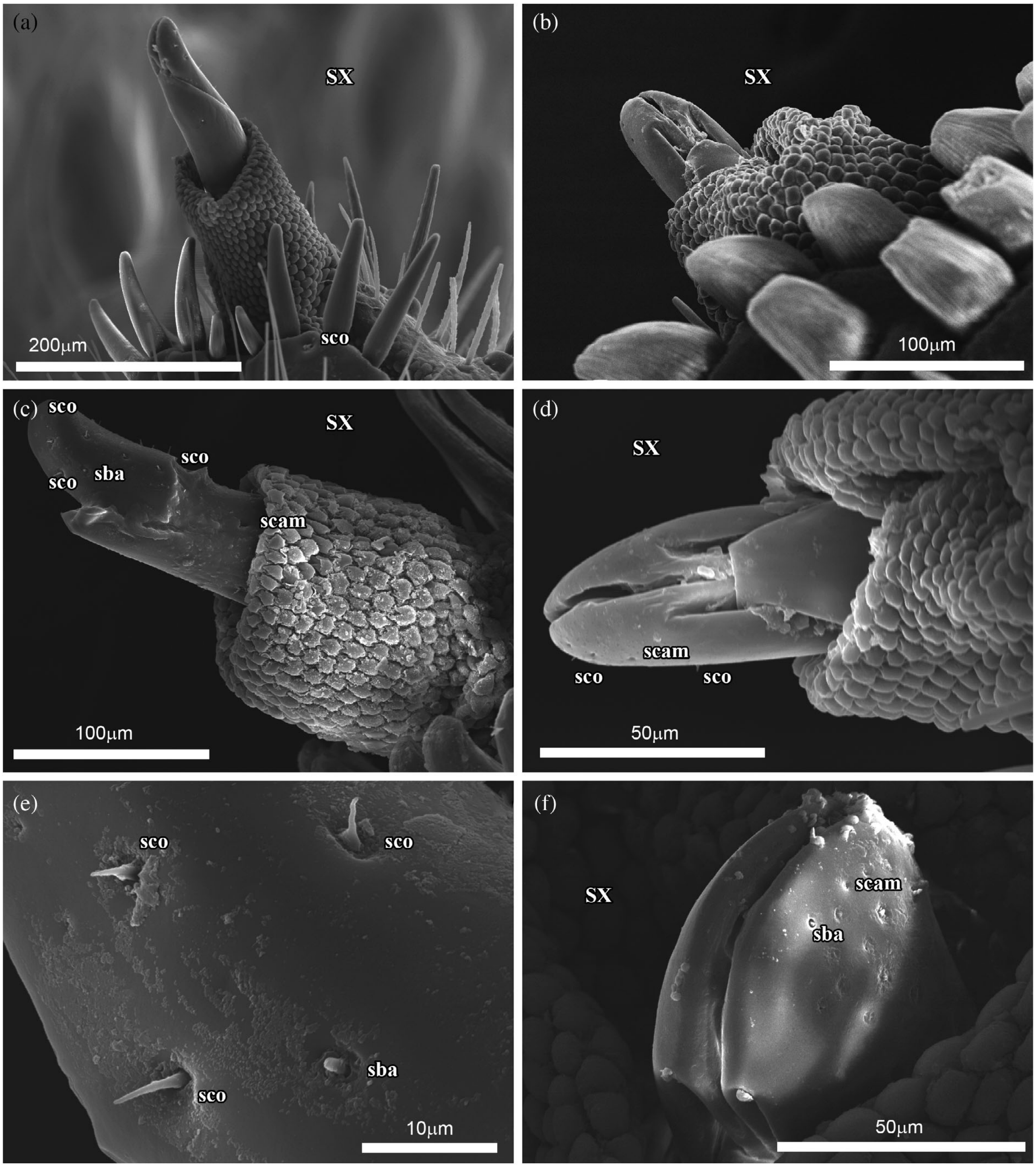

FIGURE 9 Scanning electron micrographs of abdominal segment X in third instar larvae of different antlion species. (a) *Gymnocnemia variegata*, lateral-ventral view; (b) *Myrmeleon inconspicuus*, lateral-ventral view; (c) *Macronemurus appendiculatus*, lateral view; (d) *Myrmeleon inconspicuus*, ventral view; (e) *Macronemurus appendiculatus*, lateral view; (f) *Synclisis baetica*, lateral-ventral view. sba, sensilla basiconica; scam, sensilla campaniformia; sco, sensilla coeloconica; SX, abdominal segment X

already been described for nearly all the larvae studied with SEM (Satar et al., 2006, 2014, b; Lipovšek Delakorda et al., 2009; Devetak et al., 2010a, 2010b, 2013; Tusun, 2020). While, sensilla coeloconica has been also registered in the maxillae of *Cueta lineosa* (Tusun, 2020), we provide evidence of their presence in all the studied taxa. Devetak et al. (2013) already reported the sensilla campaniformia located on the basal area of the mandibles of *M. trigrammus*.

The presence of sensilla placodea, which occur in various regions of the body of these larvae, such as the granular surface of the insertion area of the mandibles in the cephalic capsule, had never been noted before for this group. These structures are only alluded to in Doflein (1916) for *E. nostras*, by naming them "scales," and in Principi (1943, 1947) for *M. inconspicuus* and *S. baetica*, where she comments that there exist placoid formations that could be sensilla but had never been described as such.

For the first time, sensilla have been found in the interior of the food canal, a part of the larvae never studied through SEM before. The structure with large pores located on the lateral part, seems to fulfill a chemoreceptor function; this surface is herein also noted for the first time for these larvae. The sensilla placodea that appear on the ventral area of the cephalic capsule, on the mentum and the cardum are also new data.

The pronotum presents a surface described until now as granular (Devetak et al., 2010a, 2010b; Satar et al., 2006; Satar, Tusun, & Aykut, 2014). As has been indicated, we provide evidence that they are in fact sensilla placodea because in that region there are no other types of sensilla. However, because of the body position the larvae take when stalking (slightly hunched, with the pronotum at same level or higher than the head, occasionally even protruding above the surface of the substrate), and because of the sclerotization of the pronotum, it becomes evident that sensorial input from that region is highly necessary for the larvae.

Between the tarsal claws, the larvae have two type I sensilla trichodea, although the only member of the tribe Dendroleontini examined in this study, *T. relictus*, presents type II sensilla trichodea between the tarsal claws of the metathoracic legs; this does not occur in any of the other treated species. It is not clear, yet, if this trait has phylogenetic importance. What have been named type II sensilla trichodea in this work have been treated in previous articles as sensilla chaetica for *M. yemenicus*, *N. microstenus* and *M. trigrammus* (Devetak et al., 2010a, 2010b, 2013). Also on the legs, close to the tarsal claws, sensilla campaniformia have been identified, that were already observed in the European species *N. microstenus* (Devetak et al., 2010a).

On the odontoid processes, the presence of sensilla had never been noted before, and the observation of sensilla campaniformia is a new finding for these larvae.

Lipovšek Delakorda et al. (2009) and Devetak et al. (2010a) document sensilla campaniformia on the ventral region of abdominal segment IX for European species *N. microstenus*, despite the presence of sensilla campaniformia had never been indicated before on the rastra. The sensilla coeloconica are recorded for the first time in the ventral region in this work, although in *S. ledereri*, a sensillum coeloconicum can be seen on the images of the surface of the rastra (Satar, Tusun, & Aykut, 2014), though it is not referred to in the description.

The retractable abdominal segment X had never been studied using SEM; thus the sensilla found here (sensilla basiconica, sensilla campaniformia and, the most frequent, sensilla coeloconica) had never been recorded before.

Our results show that a dentate surface is located along the edge of maxillae, on the area of contact with the mandibles, coinciding with a series of parallel notches found in the mandible. This structure is now recorded in various species of different tribes, suggesting it is widespread in the group and the "matching" nature of the dentate-notched surfaces in maxillae/mandible point to a sophisticated adaptation to keep both structures tightly attached during feeding, reinforcing the food canal.

Dentate surfaces on the mouthparts have been previously mentioned for *Distoleon tetragrammicus* (Satar et al., 2006), yet, the exact shape of this structure remained unclear. Devetak et al. (2013), also mentioned short denticles on the mandibles of *M. trigrammus*, but they do not correspond to the structure described here. Lipovšek Delakorda et al. (2009) and Devetak et al. (2013) indicate the presence of digitiform sensilla on the mandible of *M. formicarius* and *M. trigrammus*, respectively. However, these sensilla were not found in any of the specimens studied in this work.

In addition to the sensilla studied and described in this work, all the setae that are present on these larvae are also tactile/mechanosensory. Since Doflein (1916), all setae were considered tactile/mechanosensory structures. Therefore, the body surface of these larvae is equipped with densely spaced sensory receptors. Regarding setae described in other works (e.g., Devetak et al., 2013; Lipovšek Delakorda et al., 2009; New, 1989), apart from the aforementioned function, plumose setae are used by the larvae to cover themselves with soil debris, thus providing them with camouflage; the digging setae, as the name indicates, are used by the larvae to bury themselves; the dolichasters probably also fulfill functions related to covering themselves and retaining soil debris for concealment. As for the sensilla, the coeloconica, placodea and basiconica fulfill chemoreceptor and olfactory functions (Devetak et al., 2013; Römer, 2003; Zacharuk, 1985); those situated on the cephalic region (palpi, antennae, and mandibles) and the pronotum probably serve in prey detection, as has been suggested in other works dealing with this and other animal groups (Devetak et al., 2013; Galizia, 2008; Glendinning, 2008; Koch, 1983; Zacharuk, 1985). The sensilla trichodea of the legs are considered mechanoreceptors (Doflein, 1916; Römer, 2003), probably related to the detection of vibrations in the substrate. The sensilla situated subterminally on the abdomen, including those of the odontoid processes and the rastra are likely associated with excavation control: with the sensilla campaniformia in a mechanosensory role and the sensilla coeloconica and basiconica in a chemosensory role (Devetak et al., 2010a, 2013; Römer, 2003). The chemoreceptive sensilla coeloconica and basiconica, and the mechanoreceptor sensilla campaniformia of abdominal segment X, are probably used for the detection of an optimal substrate for burying themselves and secrete their coccoon's silk.

Obviously, larvae possess an extensive sensory equipment to detect movements in the substrate, size and type of prey and possible dangers; it may also help finding a suitable place in which to bury themselves, build their traps, locate the right place to perform them, or the appropriate substrate to lie in wait and secrete silk to make the cocoon. The density and placement of setae and sensilla of these larvae, as well as the possession of ocular tubercles that can briefly expose them on the surface, suggest a high degree of specialization and adaptation for life in granulose substrates of the soil, be it in caves, under rocks, in trees, in open surroundings or inside sand, acquiring completely psammophilous lifestyles.

5 | CONCLUSIONS

Antlion larvae have a complex tegumentary sensorial equipment, in which six types of sensilla and two other specialized tegumentary structures have been identified in 29 species of 18 genera. They show similar patterns in terms of occurrence and density in all the studied species.

For the first time, some regions of the larval body have been studied using SEM, such as the surface of the food canal which bears sensilla coeloconica, and the abdominal segment X, that bears three types of sensilla. A novel porous texture with chemoreceptor function has been identified in the base of mandibles, and sensilla placodea are newly reported on antlion larvae, being present on the mandibular base, pronotum, mentum, and cardum.

As well, new locations of sensilla coeloconica (e.g., on rastra) and sensilla campaniformia (e.g., on odontoid processes) are noted.

A mechanism of dentate-notched surfaces that anchor maxillae and mandible, reinforcing the food canal, is detailed. All sensilla present, in addition to ocular tubercles for light caption, and their great muscular system, confer to these larvae an extraordinary predation capacity to success hunting and living in such harsh environments.

ACKNOWLEDGMENTS

We thank María Berenit Mendoza Garfías (Laboratorio de Microscopía Electrónica y Fotografía de la Biodiversidad Instituto de Biología, Universidad Nacional Autónoma de México [IBUNAM], Mexico City, Mexico) and Ana M. Vicente (Centro Nacional Microscopía electrónica Universidad Complutense Madrid [CNME-UCM], Madrid, Spain) for their help and support during this study. This research has been partially funded by projects CGL2010-22267-C07-05 (Spanish Ministry of Sciences and Innovation) and IN207517 (Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica, UNAM). F. A. received support from a postdoctoral grant (CT53/16-CT54/16) at the Instituto de Biología, Universidad Nacional Autónoma de Mexico.

AUTHOR CONTRIBUTIONS

Fernando Acevedo Ramos: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review and editing. **Víctor Monserrat:** Conceptualization; funding acquisition; investigation; project administration; resources; supervision; writing-original draft; writing-review and editing. **Atilano Contreras-Ramos:** Funding acquisition; project administration; resources; writing-original draft. **Sergio Pérez-Gónzalez:** Conceptualization; formal analysis; investigation; supervision; visualization; writing-original draft; writing-review and editing.

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How to cite this article: Acevedo Ramos F, Monserrat VJ, Contreras-Ramos A, Pérez-González S. Comparative study of sensilla and other tegumentary structures of Myrmeleontidae larvae (Insecta, Neuroptera). *Journal of Morphology*. 2020;281: 1191–1209. https://doi.org/10.1002/jmor.21240