Arthropod Structure & Development 64 (2021) 101085

Contents lists available at ScienceDirect

Arthropod Structure & Development

journal homepage: www.elsevier.com/locate/asd

The morphology of *Colpocephalum pectinatum* (Phthiraptera: Amblycera: Menoponidae) under scanning electron microscopy

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A R T I C L E I N F O

Article history:
Received 6 May 2021
Accepted 25 June 2021
Available online xxx

Keywords:
Colpocephalum pectinatum
SEM
Menoponidae
Morphology

A B S T R A C T

Here, we describe under scanning electron microscopy (SEM) the morphology of *Colpocephalum pectinatum* (Phthiraptera, Menoponidae), an ectoparasite found in burrowing owls, *Athene cunicularia*. We devote particular attention to the morphology of the main structures of the head (antennae and mouthparts) and legs (tarsi and femoral ctenidia). Moreover, we describe the main peripheral sensory organs, located in the labial palpi and the distal end of antennae. We also detected that the structure of antennae and antennal sensilla arrangement are very similar to that described for other *Colpocephalum* and Menoponid species, and we discuss the function of each type of sensilla. We suggest that SEM studies combined with other microscopy and physiological techniques could be useful for elucidate the function of each structure, lice behaviour, as well as their taxonomy.

1. Introduction

The genus *Colpocephalum* Nitzsch, 1818 (Phthiraptera: Amblycera: Menoponidae), also known as the *Colpocephalum* complex, includes about 135 chewing lice species parasitizing a wide variety of birds (Galliformes, Cuculiformes, Columbiformes, Gruiformes, Ciconiiformes, Pelecaniformes, Accipitriformes, Falconiformes, Strigiformes, Psittaciformes and Passeriformes) (Price et al., 2003). The main combination of morphological features that characterizes this group are: head with black or strong pre-ocular and occipital nodi, a characteristic pattern of dorsal head sensilla and setae, typical oblong strongly pigmented postnotum and presence of a comb of ctenidia on the sternites and femora (Clay, 1969; Price et al., 2003; Catanach et al., 2018).

Two lineages are recognized and currently treated as subgenera within the *Colpocephalum* complex: *Aquiligogus* from hawks (Accipitriformes) and falcons (Falconiformes) and *Neocolpocephalum* from hawks and owls (Strigiformes), respectively (Catanach et al., 2018). *Colpocephalum pectinatum* Osborn, 1902 has been reported as ectoparasite of various Strigiform host species, including the burrowing owl (*Athene cunicularia*), its type-host, through most of its distribution range: e.g., USA (Thompson, 1950; Skoruppa et al., 2006), Mexico (Bolaños-García et al., 2018), Brasil (Oliveira da Silva et al., 2009) and Argentina (Daciuk et al., 1981). *C. pectinatum* is characterized by a particular chaetotaxy and dimensions and by male genitalia lacking lateral serrations along the basal half of the penis (Price and Beer, 1963) (Fig. 1). Nevertheless, the placement of *C. pectinatum* in either of the above-mentioned subgenera is unclear, and the whole group needs to be revised.

Scanning Electron Microscopy (hereafter SEM) studies provide new details on the morphology of louse specimens because of the magnification and the multiple angles from which we can observe such specimens. This information about louse structures can help to better understand the physiology and behaviour of these ectoparasites. Nevertheless, there are very few SEM studies on the genus *Colpolcephalum* (Pérez et al., 1996; Dik et al., 2018; Antonello et al., 2020). Thus, the aim of this study was to analyze under SEM the morphology of *C. pectinatum* collected in individuals of burrowing owls from Argentina, in order to provide a more detailed description.

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https://doi.org/10.1016/j.asd.2021.101085
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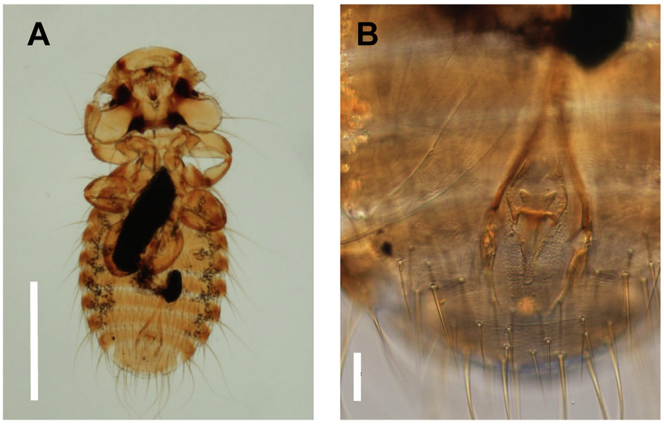


Fig. 1. A. *Colpocephalum pectinatum*. Habitus of an adult male. Scale bar: 500 μm. **B**. Male genitalia. Scale bar: 50 μm.

2. Materials and methods

The study area includes the urban area of Bahia Blanca, located south of the province of Buenos Aires (Argentina), and its rural surroundings. Here, a continuous monitoring of a breeding population of burrowing owls has been conducted for more than ten years (Rebolo-Ifrán et al., 2017 and Luna et al., 2020 to see details). During the breeding periods (November–February) of 2016–2017 and 2017–2018, we searched for ectoparasites in 869 burrowing owls. With this purpose, two observers detected and collected all types of ectoparasites using a systematic approach, devoting 5 min of search to each specimen, and examining all parts of the bird's body in order to collect all possible ectoparasites detected in the skin and between the feathers.

The collected ectoparasite specimens were fixed in 97% ethanol. Once in the laboratory, lice were treated and mounted in Canada balsam following the technique described by Palma (1978), and identified as *Colpocephalum pectinatum*, based on the descriptions of Price and Beer (1963), Clay (1969), and Price et al. (2003). Specimens were examined and photographed with a Nikon Eclipse 80i, light microscope equipped with DIC and a Nikon DS digital camera.

After their examination and identification, ten adult female and ten adult male lice preserved in ethanol were selected for observation under SEM following the next protocol: (i) storage in a mixture of 70% ethanol and 30% ether during three days (Soler-Cruz and Martín-Mateo, 2009), (ii) cleaning with an ultrasound equipment (20 min with medium frequence and low intensity: 30%), (iii) dehydration in a gradient ethanol series and acetone (Abolafia et al., 2002), (iv) critical point drying, (v) mounting on metal stubs using carbon adhesive pads, and (vi) sputter-coating with gold. Finally, specimens were observed with a Zeiss Merlin scanning electron microscope (Carl Zeiss, Germany). Nomenclature of the different parts of the lice head follows that given by Symmons (1952).

3. Results

The head has a complex shape with lateral holes for harbouring the antennae (Fig. 2A). Simple eyes can be seen ventrally, between antennae and maxillary palpi (Fig. 2B). Laterally, the head has a triangular shape (Dik et al., 2018) flattened in front and wider in the temporal region (Fig. 2C). Antennae are four-segmented (Fig. 2E). The cuticle of antennal segments has a scaly appearance (as in other parts of the head) and the last segment ends in a circular cluster of 16 sensilla of various types: basiconic and coeloconic, including one tuft organ) with another smaller triangular cluster of 4 sensilla very close (Fig. 2F).

Mouth parts can be seen in Fig. 3. The labrum is centrally divided and the tips of the mandibles are bidentate (Figs. A and D). The galea is located between the mandibles and hypopharynx (Fig. I), and it is armed with numerous conic and curved tooth-like cuticular formations. The hypopharynx (Figs. E–G) has a frayed anterior end forming the hypopharyngeal comb. Labial palpi (Fig. H) are very short and in their tips five basiconic sensilla can be found. On the contrary, maxillary palpi (Fig. B–C) are long and present a cluster of 13 basiconic sensilla on their tips, together with a long subterminal seta.

Subocular comb row (Fig. 2D), abdominal (Fig. 5E) and femoral ctenidia (Fig. 4 (C,D,F) are formed by a number of rows of spine-like structures.

The mesothorax (Fig. 4B) is small compared with prothorax and metathorax, and seems to be less scletorized than the other thoracic segments. The mesonotum and some mesonotal anterior setae can be seen in Fig. 4E. Pretarsi are long and bear two terminal claws (Fig. 4H–J), with a fluted inner margin (Fig. 4J), which could improve fixation to host feathers. In the basis of the pretarsus we can see the empodium, with a membranous appearance (Fig. 4J).

Abdominal spiracles are simple (Fig. 5A–C). In Fig. 5 F–I, we can observe the terminal part of the abdomen of the adult male and female, respectively, with their characteristic trichoid sensilla.

4. Discussion

Even if *Colpocephalum* is one of the best studied menoponid genera, our knowledge on the relationships within the *Colpocephalum*-complex is still incomplete. SEM allows us to observe lice structures, not only at high magnification, but also from diverse angles and perspectives, therefore improving our knowledge on the morphology of these ectoparasites. This may be of particular interest for differentiating lice head shape with a three-dimensional basis within the *Colpocephalum*-complex and even in other menoponid genera. We must take into account that light microscopy does not allow for the observation of the lateral morphology of mounted specimens (e.g., as in most Phthirapteran species, the eyes in *C. pectinatum* are small and simple, but they are not visible when observing mounted specimens under light microscopy). Other features, such as the placement of the ocular and preocular setae may be of systematic importance in the Ischnocera, but the utility of this character is limited due to the two-dimensional nature of slide-mounted specimens.

Recently, a series of half-moon-shaped structures with bilateral symmetry has been described in the ventral region of the posterior margin of the head of *C. spineum*, a louse species parasitizing the common fregatebird (Antonello et al., 2020), but they were absent in *C. pectinatum*. Further studies focussed on other *Colpocephalum* species and Amblyceran genera are needed to address the question whether such structures have taxonomic and/or functional relevance.

The mouthparts of Amblyceran lice are essentially modified to suck blood (Johnson and Clayton, 2003) and members of Menoponidae feed host blood in varying degrees or frequency (Kumar et al., 2017). This extreme has not been reported in members of the genus *Colpocephalum*, but a predatory behaviour of *Colpocephalum turbinatum* (a parasite of the domestic pigeon, *Columba livia*) was suggested, as adult lice were observed eating their own eggs and nymphs (Nelson, 1971). In the case of *C. pectinatum*, the sharp mandibles and the tooth-like formations of the galea, could erode the host skin or feathers. Rearing specimens of this louse

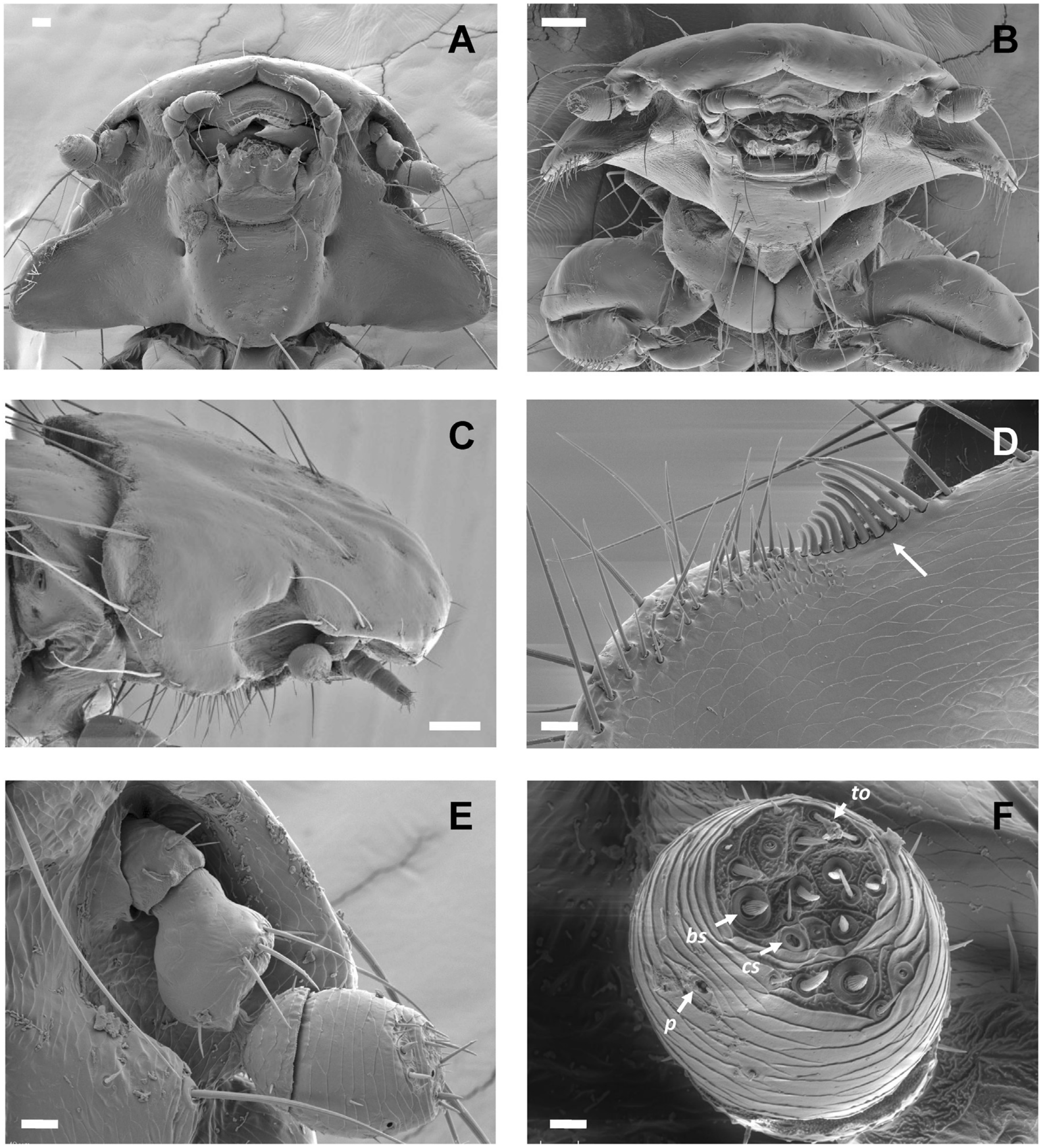


Fig. 2. **A**. Female. Ventral view of the head. Scale bar: 20 μm. **B**. Male. Frontal view of the head. Scale bar: 50 μm. **C**. Female. Lateral view of the head. Scale bar: 50 μm. **D**. Female. Subocular comb row. Scale bar: 10 μm. **E**. Female. Four-segmented antenna. Scale bar: 10 μm. **F**. Male. Detail of the tip of the antenna showing pore or pit organ (p), basiconic sensilla (bs), coeloconic sensilla (cs) and tuft organ (to). Scale bar: 5 μm.

species (both *in vivo* and *in vitro*) would allow us to elucidate its haematophagous nature.

All sensilla are cuticular structures encapsulating and protecting neurons which respond to specific stimuli (Ortega Insaurralde et al., 2019). Coeloconic sensilla have morphological features consistent with an olfactory function (Crespo and Vickers, 2012). Basiconic sensilla are also chemoreceptors, being round-end basiconic ones gustatory or contact chemoreceptors and tuft organs are thermo-hygroreceptors (Ortega Insaurralde et al., 2019). The morphology of the antennae is quite similar and maintained throughout the Phthirapteran suborders and families, being characterized by the concentration of sensilla in the distal end (Baker and Chandrapatya, 1992; Soler Cruz and Martín Mateo, 1998; Ortega Insaurralde et al., 2021).

The general antennal shape and structure found in *C. pectinatum* is very close to those described for other menoponid genera (Clay, 1969; Ayra and Singh, 2012). This may also be applied to the arrangement of sensilla, which is very similar to that described for *Colpocephalum nanum* (Dik et al., 2018). Moreover, the general antennal shape and structure in both species is very close to those described for other menoponid genera (Clay, 1969; Ayra and Singh, 2012). Contrary to what happens in Menoponidae, Boopidae, Ricinidae and Laemobothriidae, taxa belonging to Trimenoponidae and Gyropidae show considerable diversity in the form of the antennal sense organs, even within genera (Clay, 1970). Size differences in antennal sensory structures of body and head lice (Anoplura) have been reported and related to adaptation to different biotopes (Ortega Insaurralde et al., 2021).

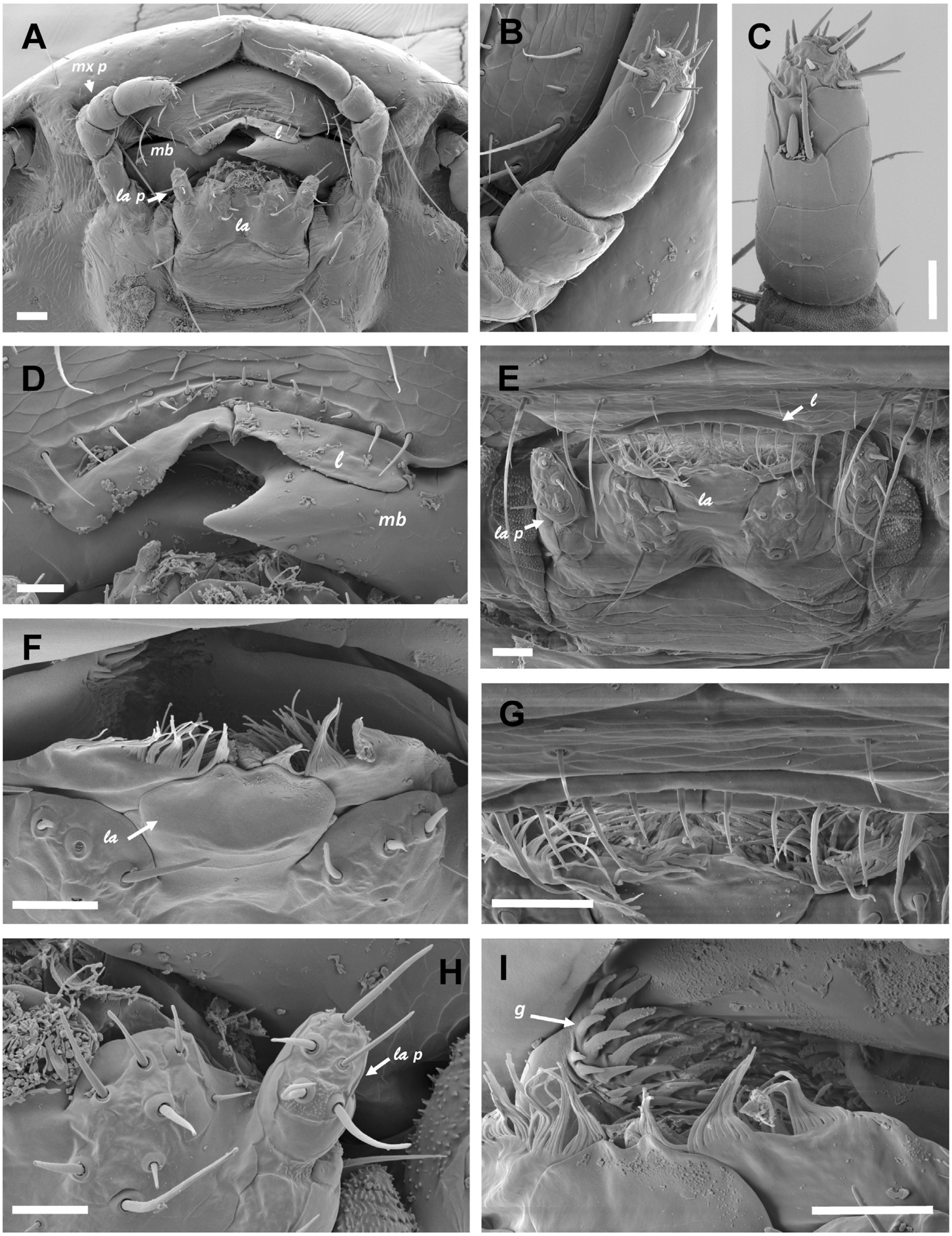


Fig. 3. **A**. Female. Mouthparts. Scale bar: 20 µm. **B**. Female. Maxillary palpus (ventral view). Scale bar: 10 µm. **C**. Female. Maxillary palpus: detail of last segment (lateral view). Scale bar: 10 µm. **D**. Female. Labrum and mandibles. Scale bar: 10 µm. **E**. Female. Labium and labial palpi. Scale bar: 10 µm. **F**. Male. Hypopharyngeal comb and labium. Scale bar: 10 µm. **G**. Hypopharyngeal comb and labium (frontal view). Scale bar: 10 µm. **H**. Female. Labial palpus. Scale bar: 10 µm. **I**. Male. Galea, hypopharynx and labium. Scale bar: 10 µm. Abbreviations: g: galea; l: labrum; la: labium; la p: labial palpus; mb: mandibles; mx p: maxillary palpus.

The size and shape of the mesothorax could facilitate certain articulation at the middle level of the thorax. We need to analyse if the spacing of spines in the combs and ctenidia shows a close relationship with the diameter of host feather barbs in order to assess if the subocular comb row, together with abdominal and femoral ctenidia, can improve fixation to host feathers, complementary to that provided by mandibles and tarsal claws, as an adaptation against dislodgement by the host (preening) (Humphries, 1967). In several amblyceran genera (e.g., *Bonomiella* and *Microctenia*) the shape of the tarsal claws may be used as a criterion for taxonomic identification

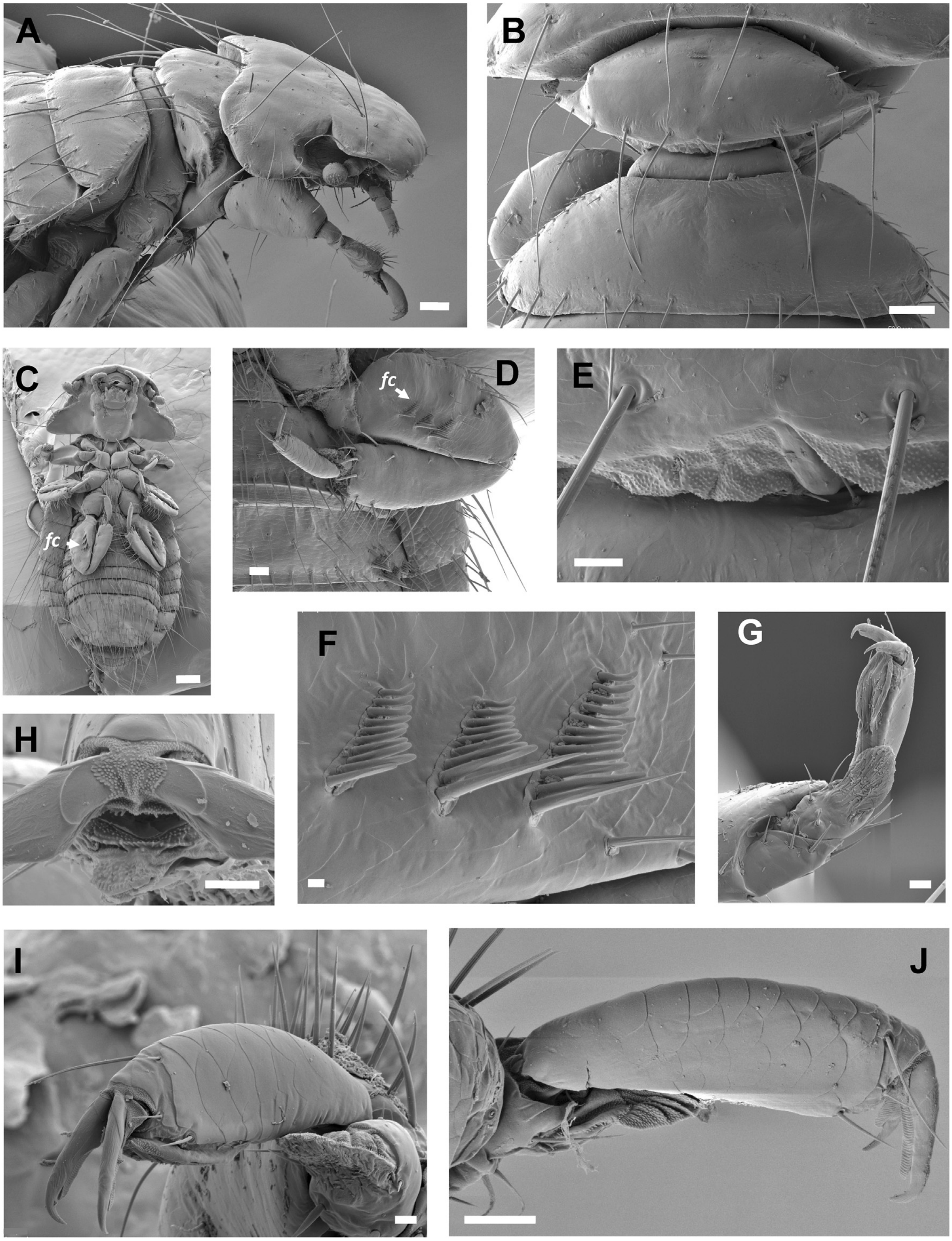


Fig. 4. A. Female. Lateral view of head and thorax. Scale bar: 50 μm. **B**. Female. Dorsal view of the thorax. Scale bar: 50 μm. **C**. Female. Habitus (ventral view) showing femoral ctenidia (fc). Scale bar: 100 μm. **D**. Male. Femoral ctenidia (fc) on femur III. Scale bar: 100 μm. **E**. Female. Mesonotal plate. Scale bar: 10 μm. **F**. Male. Detail of femoral ctenidia. Scale bar: 3 μm. **G**. Ventral view of the tarsus. Scale bar: 10 μm. **H**. Female. Tarsal claws. Scale bar: 5 μm. **I-J**. Female. Tarsus and empodium. Scale bars: 5 μm and 15 μm, respectively.

(Clay, 1969). Amblyceran lice show less capacity to remain attached to the host feathers and are less phoretic than Ischnoceran, but are more mobile, particularly off the host, therefore increasing their own dispersal capacity (Bartlow et al., 2016).

An extensive study of antennae over the genus *Colpocephalum* would confirm if differences of arrangement and size in sensory organs exist between species belonging to *Aquiligogus* and *Neocolpocephalum* subgenera. Extending such studies to other Menoponid and Amblyceran genera will help us to better understand the sensorial function in this suborder of lice and could provide us new structures and/or structure arrangements with taxonomic value, possibly at suborder and/or family levels (Clay, 1970; Baker and

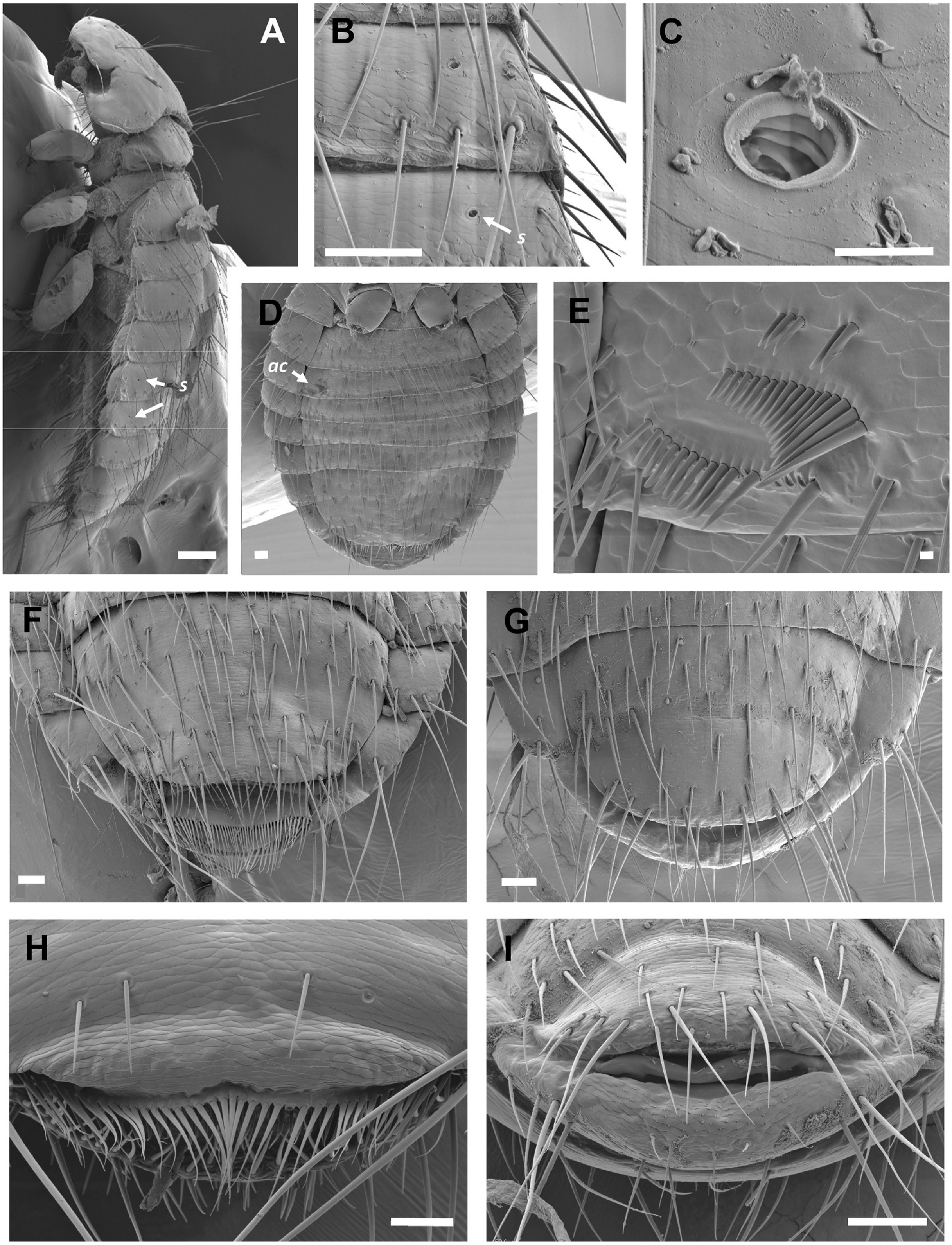
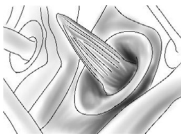
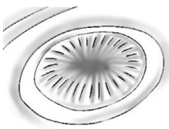
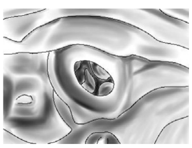
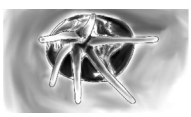
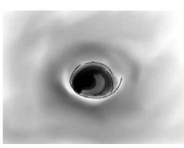
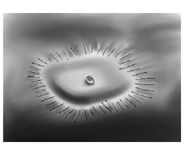


Fig. 5. **A**. Female. Habitus (lateral view) showing spiracles (s). Scale bar: 100 μm. **B**. Female. Dorsolateral view of the abdomen showing spiracles. Scale bar: 50 μm. **C**. Female, Detail of the spiracle. Scale bar: 5 μm. **D**. Male. Ventral view of the abdomen with ctenidia (ac) in the third abdominal sternite. Scale bar: 30 μm. **E**. Male. Detail of the abdominal ctenidia. Scale bar: 3 μm. **F**. Female. Abdominal end (ventral view). Scale bar: 25 μm. **G**. Male. Abdominal end (ventral view). Scale bar: 30 μm. **H**. Female. Abdominal end (dorsal view). Scale bar: 25 μm. **I**. Male. Abdominal end (dorsal view). Scale bar: 50 μm.

Table 1
Presence of the different types of sensilla in Phthirapteran suborders and families. References included are not exhaustive, but illustrative. Our goal was to include as many Phthirapteran taxa as posible. Artwork by Rubén Pérez.

SENSILLA TYPE		PHTHIRAPTERAN TAXA	REFERENCES
	basiconic	**Rhynchophthirina**: Haematomyzidae **Anoplura**: Pediculidae, Echinophthiriidae **Amblycera**: Gyropidae, Menoponidae **Ischnocera**: Trichodectidae	Baker and Chandrapatya (1992); Ortega Insaurralde et al. (2019); Ortega Insaurralde et al. (2021); Leonardi et al. (2012); Clay (1969); Arya and Singh (2012); Present study; Martino et al. (2010); Sebei et al. (2004); Turner et al. (2002); Clarke (1990)
	placodean	**Ischnocera**: Philopteridae	Pérez (1990); Soler Cruz and Martín Mateo (1998); Ahmad et al. (2014); Agarwal et al. (2011)
	coeloconic (pit organ)	**Rhynchophthirina**: Haematomyzidae **Anoplura**: Echinophthiriidae, Haematopinidae, Enderleinellidae, Hoplopeuridae, Linognathidae, Pediculidae, Polyplacidae, Pedicinidae, Phthiridae **Amblycera**: Menoponidae, Gyropidae, Boopidae, Ricinidae, Laemobothriidae, Trimenoponidae	Baker and Chandrapatya (1992); Clay (1969); Present study; Dick et al. (2018) Clay (1969); Clay (1970); Arya and Singh (2012); Martino et al. (2010)
	coeloconic (tuft organ)	**Rhynchophthirina**: Haematomyzidae **Anoplura**: Pediculidae **Amblycera**: Menoponidae, Gyropidae **Ischnocera**: Trichodectidae	Baker and Chandrapatya (1992); Present study; Martino et al. (2010); Sebei et al. (2004); Turner et al. (2002); Soler Cruz and Martín Mateo (1998); Clarke (1990); Ortega Insaurralde et al. (2019); Ortega Insaurralde et al. (2021)
	pore	**Anoplura**: Pediculidae **Amblycera**: Menoponidae	Ortega Insaurralde et al. (2019); Ortega Insaurralde et al. (2021); Present study
	pore organ	**Rhynchophthirina**: Haematomyzidae **Anoplura**: Pediculidae **Ishnocera**: Trichodectidae	Baker and Chandrapatya (1992); Ortega Insaurralde et al. (2019); Ortega Insaurralde et al. (2021); Sebei et al. (2004); Turner et al. (2002)
	trichoidea	**Rhynchophthirina**: Haematomyzidae **Anoplura**: Echinophthiriidae; Pediculidae, **Amblycera**: Menoponidae **Ishnocera**: Trichodectidae	Baker and Chandrapatya (1992); Leonardi et al. (2012); Clarke (1990); Ortega Insaurralde et al. (2019); Arya and Singh (2012); Present study

Chandrapatya, 1992) (Table 1). SEM studies may be time consuming, particularly for sample cleaning and preparation, but they are very useful for improving our knowledge on different aspects of the biology of Phthiraptera and other ectoparasites. Further studies on the diet of this species, coupled with confocal microscopy and electrophysiological studies as well, could confirm this hypothesis and provide some insights on the function of the different mouthparts.

Author contributions

A.L., A.*P. and* P.R.V. obtained samples; A.S. performed slide mounting and identification of lice. G.M.L. and J.M.P. planned, designed, and performed the study. J.M.P. wrote the first draft of the manuscript. All authors revised the manuscript and approved its final version.

Acknowledgements

The authors' research activities were partially funded by the PAIDI, Junta de Andalucía (RNM-118 and RNM-182 groups) and 'PAIUJA 2021/2022: EI_RNM02_ 2021' of the University of Jaén. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors. SEM pictures were obtained with the assistance of technical staff and the equipment of the "Centro de Instrumentación Científico-Técnica (CICT)", University of Jaén.

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