

Antennal Morphology of the Endogean Carabid Genus *Typhlocharis* (Coleoptera: Carabidae: Anillini): Description of Sensilla and Taxonomic Implications

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ABSTRACT The antennal morphology and chaetotaxy were studied in 52 species of the endogean carabid genus *Typhlocharis*, using scanning electron microscopy and light microscopy. The antennae are composed of 11 antennomeres (scape, pedicel, and nine flagellomeres). We found considerable variation between species in the third antennomere, with short-stem and long-stem forms, and flagellomere morphology, distinguishing two morphs: rounded (subovoid, subspheric and subquadrate, morph 1) and reniform shapes (morph 2). Antennal sensilla are grouped in six types of *sensilla trichodea*, three types of *sensilla basiconica*, one type of *sensilla coeloconica*, and one type of *sensilla campaniformia*. The distribution of sensilla along the antennomeres is described. The “rings” of trichoid sensilla in the antennomere body are affected by its shape and there is interspecific variation in the pattern of *sensilla coeloconica* in antennomere 11°, a novelty for the genus. The types of sensilla found in *Typhlocharis* are compared to those described in other Carabidae and the potential functionality and taxonomic interest of those variable antennal features are discussed. A correlation between the flagellomere morphology and the presence/absence of a stridulatory organ is suggested. The study also allowed comparing the observation of antennal features by SEM and light microscopy. *J. Morphol.* 000:000–000, 2013. © 2013 Wiley Periodicals, Inc.

KEY WORDS: antennae; morphology; sensilla; Carabidae; *Typhlocharis*; microscopy

INTRODUCTION

The genus *Typhlocharis* Dieck, 1869 (Coleoptera, Carabidae, Trechinae, Anillini) is the most diverse endogean carabid of the Mediterranean region. It is distributed throughout the Iberian Peninsula and North Africa (Morocco and Tunisia). There are 56 species currently recognized (Pérez-González and Zaballos, 2013); all of them characterized by numerous adaptations to the endogean environment, such as tiny size (ranging between 0.9 and 2.9 mm), elongate, depressed, rectangular-shaped body, lack of pigmentation, anophthalmia or extensive development of sensorial setae, especially those of the elytral umbilicate series (Jeannel, 1937). Despite the number of species described in

the last 30 years has increased almost exponentially (Zaballos and Pérez-González, 2010; Ortuño and Gilgado, 2011), several morphological aspects with potential taxonomic value had received little attention or remain unconsidered within the genus (Pérez-González and Zaballos, 2012).

Typhlocharis inhabits the uppermost horizon of soil (horizon A), with the highest percentage of organic matter and the soil horizon below that (horizon B), with a higher percentage of clay, sand, and other mineral components (Ortuño, 2000) from 10 to 50 cm deep, and frequently under big, deeply buried boulders. Most of the species' ecology or environmental preferences are still unknown, but they appear to be strongly conditioned to soil humidity and it is known they can bear long periods (more than 30 days) completely submerged in water (Ortuño, 2000; Zaballos and Pérez-González, 2011b). This survival ability, and the environment where they live, led Ortuño and Gilgado (2011) to propose a dispersal model for the genus based in hydrochoric mechanisms, that is, helped by water movements, which would partially explain the widespread distribution of some species of the genus. Their diet and feeding habits are also unknown. It is probable that some of the larger and more agile species (e.g., *T. carinata* Serrano and Aguiar, 2006; *T. algarvensis* Coiffait, 1971) could occasionally be predators, as occurs in other endogean Anillini (predation over springtails has been recorded for the genus *Geocharis* by Zaballos, 1990), but the body proportions and slow movements of the majority of the species may suggest detritivory.

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Inter- and intraspecific communication mechanisms are unclear. The perception of the environment using mechanoreception and chemoreception mechanisms is emphasized in the particular conditions of the endogean habitats (absence of light, high humidity, reduced spaces, and obstacles), where the visual information becomes unnecessary, but there exists a high variety of tactile, chemical, and audible stimuli. The main sensorial functions are assumed by sensilla, present all over the body surface. The most important tactile sensilla appears in head, pronotum, and elytra, particularly in the latter, where the umbilicate series comprises from four to eight long setae (Zaballos and Ruíz-Tapiador, 1997), parallel with each other (perpendicular to longitudinal axis) and articulated in basis which allows great mobility. In antennae, sensilla are especially diversified and also cover other functions, such as chemoreception (Ploomi et al., 2003). Behavior of antennal cleaning was observed in live specimens of *Typhlocharis portilloi* Zaballos, 1991, using the protibial cleaner organ in a similar way to that reported in *Geocharis* (Zaballos, 1990).

Antennal morphology, with reference to the different types and location of sensilla in each antennomere, has been studied and described in several species of Carabidae (e.g., Daly and Ryan, 1979; Kim and Yamakasi, 1996; Merivee et al., 2001; Giglio et al., 2008), including some Trechinae (Juberthie and Massoud, 1977, 1980; Merivee et al., 2000, 2002) and Anillini (Ortuño and Sendra, 2007, 2010). The information given by these works indicates that antennae are potentially useful structures as taxonomic tools. It is necessary that a systematized study of the variation patterns of antennal structures, little considered in *Typhlocharis* until now, be undertaken.

The aim of this work is to present a detailed description of morphology and chaetotaxy of the antennae in genus *Typhlocharis*, discussing the utility of these characters in the interpretation of relationships between species. Moreover, it will suppose a base tool in future works on the relation mechanisms in endogean carabids and taxonomy of the genus.

MATERIAL AND METHODS

Insects

Antennal morphology and chaetotaxy were revised in 52 species of *Typhlocharis* from collections J.P. Zaballos (Universidad Complutense de Madrid), A. Serrano (Universidade de Lisboa), and museums (Museum für Naturkunde, Berlin and Museum national d'Histoire naturelle, Paris; Table 1).

The observations were done mainly by light microscopy (for all studied species). Two species (*T. prima* Pérez-González and Zaballos, 2013 and *T. farinosae* Zaballos and Ruíz-Tapiador, 1997), representative of the two more divergent morphologies observed, were selected to confirm the morphological details by

scanning electron microscopy. The protocols for preparation of specimens are detailed below.

Light Microscopy

At least two specimens (male and female) were selected for all the species with large enough series. They were hydrated, then rinsed in lactic acid (approx. 24 h). Observations were done with binocular microscope Zeiss KF-2, Germany, in cavity slides, with the specimen submerged in lactic acid to allow manipulation and observation from different angles.

Scanning Electron Microscopy

Six specimens of *T. prima* (fresh, untreated) and two specimens of *T. farinosae* (previously gold-coated in 1997) were selected for SEM techniques. Untreated specimens were cleaned by successive washing in soapy water, Scheerpeltz liquid and lactic acid, before a final rinse and subsequent dehydration in graded ethanol series (70%, 90%, and 100%), then air-dried and stored at 37°C. They were mounted in the distal end of a copper wire glued with water-soluble dimethyl hydantoin formaldehyde resin (Bameul, 1990) to electron microscope stubs. Already coated specimens were cleaned in distilled water and later rinsed in absolute ethanol. All the specimens were covered with graphite in a Cressington 108carbon/A carbon coater before being sputter coated with gold in an Emitech K550X sputter coater, Quorum Technologies (United Kingdom). Observations and photographs made using a JEOL 6400 JSM microscope (Japan).

Classification of the Sensilla

Nomenclature of sensilla follows Zacharuk (1985). Nevertheless, given that differences between *sensilla trichodea* and *sensilla chaetica* are based mainly on the width of the articular socket, but both are rather similar in morphology and sometimes difficult to differentiate, all types of trichoid sensilla described in this work are treated as "*sensilla trichodea*" *sensu lato*.

DESCRIPTION OF THE ANTENNAE

Antennal Morphology

Typhlocharis has moniliform antennae with 11 antennomeres, differentiated in three regions: scape (1°), pedicel (2°), and flagellum (3°–11°; Fig. 1). Every antennomere also has two regions: stem, a cylindrical base, and body, bearing the sensilla.

Scape and pedicel are both globet-shaped with spherical condyle basal joint (Figs. 1 and 2). No important morphological differences have been observed for these antennomeres within the genus, except the general proportions affecting the whole antenna. The scape is always larger and longer than the pedicel, with a shorter stem and a wider distal end which enables a good articulation of pedicel. The integument of the scape is generally smooth, but some species with a strongly marked microsculpture (e.g., *T. rochapitei* Serrano and Aguiar, 2008; *T. fozcoensis* Serrano, Aguiar and Proença, 2005; *T. navarica* Zaballos and Wrase, 1998).

Antennomere 3° is subspherical, with a longer stem than the rest of antennomeres (Figs. 1 and 3.). The length of this stem varies significantly between

TABLE 1. Antennal characters with interspecific variation

Species	Specimens observed	Flagellomere morphology	Antennomere 3° (average proportion of stem length/ antennomere body length)	Pattern of sensilla <i>coeloconica</i> (antennomere 11°)	Presence of <i>sensilla</i> <i>coeloconica</i> (antennomeres 5° and 6°)
<i>T. monastica</i>	1♂ 1♀ PTs, JPZ	Morph 1: subspheric	1.07	A	Unconfirmed
<i>T. peregrina</i>	1♂HT 1♀PT, JPZ	Morph 1: subquadrate	1.03	A	Yes
<i>T. toletana</i>	2♂ 2♀, JPZ	Morph 1: subspheric	0.63	B	Unconfirmed
<i>T. josabelae</i>	–	?	?	?	Unconfirmed
<i>T. gomezi</i>	1♂HT 1♀PT, JPZ	Morph 1: subquadrate	0.57	A	Yes
<i>T. hiekei</i>	3♂ 3♀ PTs, JPZ	Morph 1: subquadrate	0.58	A	Yes
<i>T. wrasei</i>	1♂ 1♀ PTs, JPZ	Morph 1: subquadrate	0.52	A	Unconfirmed
<i>T. passosi</i>	2♂ 2♀ PTs, JPZ	Morph 1: subquadrate	0.58	A	Unconfirmed
<i>T. fozcoaensis</i>	1♀PT, ARS	Morph 1: subquadrate	0.55	A	Yes
<i>T. bivari</i>	1♂ 1♀ PTs, ARS	Morph 1: subquadrate	0.54	A	Yes
<i>T. carpetana</i>	4♂ 3♀ PTs, JPZ	Morph 2: reniform ^a	0.72	C	Yes
<i>T. portilloi</i>	5♂ 5♀ PTs, JPZ	Morph 2: reniform ^a	0.78	C	Yes
<i>T. silvanoides</i>	1♂ 2♂ST, MNHNP	Morph 1: subspheric	0.82	A	Yes
	1♀ST, MFNB, 3♂, JPZ				
<i>T. algarvensis</i>	1♂PT 1♀, JPZ	Morph 1: subovoid	0.57	F	Yes
<i>T. fancelloi</i>	1♂ 1♀ PTs, JPZ	Morph 1: subovoid	0.56	D	Yes
<i>T. sarria</i>	2♂ (n° 15650), ARS	Morph 1: subspheric	0.46	A	Yes
<i>T. carinata</i>	4♂ 4♀ PTs, JPZ	Morph 1: subovoid	0.90	E	Yes
<i>T. paulinoi</i>	1♂ 1♀, JPZ	Morph 1: subovoid	0.71	A	Yes
<i>T. baetica</i>	1♂ 1♀, JPZ	Morph 1: subspheric	0.72	A	Yes
<i>T. pacensis</i>	1♂HT 1♀PT, JPZ	Morph 1: subquadrate	0.55	A	Yes
<i>T. aguirrei</i>	1♂HT 1♀PT, JPZ	Morph 1: subquadrate	0.67	A	Unconfirmed
<i>T. millenaria</i>	1♂HT 1♀PT, JPZ	Morph 1: subspheric	0.53	A	Yes
<i>T. furnayulensis</i>	1♂HT 4♂4♀ PTs, JPZ	Morph 1: subspheric	0.64	A	Yes
<i>T. matiasi</i>	1♂HT 1♂5♀ PTs, JPZ	Morph 1: subspheric	0.61	A	Yes
<i>T. prima</i>	1♂HT 7♂4♀ PTs, JPZ	Morph 1: subspheric	0.51	A	Yes
<i>T. secunda</i>	1♂HT 1♂1♀ PTs, JPZ	Morph 1: subspheric	0.57	A	Yes
<i>T. tertia</i>	1♂HT 1♀PT, JPZ	Morph 1: subspheric	0.78	A	Yes
<i>T. quarta</i>	1♂HT 1♀PT, JPZ	Morph 1: subspheric	0.59	A	Yes
<i>T. diecki</i>	1♂ 1♀, JPZ	Morph 1: subquadrate	0.50	C	Yes
<i>T. santschii</i>	2♂ 2♀, MNHNP	Morph 1: subspheric	1.02	C	Unconfirmed
<i>T. armata</i>	1♀HT, MNHNP	Morph 1: subspheric	0.53	A	Yes
	1♂PT 9♂ 9♀, JPZ				
<i>T. besucheti</i>	1♂ 1♀, JPZ	Morph 1: subquadrate	0.71	A	Yes
<i>T. carmenae</i>	1♂HT 1♀PT, JPZ	Morph 1: subquadrate ^a	0.66	C	Yes
<i>T. farinosae</i>	1♂HT 1♂ 2♀ PTs, JPZ	Morph 2: reniform ^a	0.63	C	Yes
<i>T. gonzaloi</i>	–	?	?	?	Unconfirmed
<i>T. lunai</i>	1♂ 2♀ PTs, ARS	Morph 1: subovoid	0.74	A	Yes
<i>T. rochapitei</i>	1♀PT (n° 16098), ARS	Morph 1: subspheric	0.61	B	Yes
<i>T. martini</i>	1♂ 1♀ PTs, JPZ	Morph 1: subquadrate	0.69	A	Yes
<i>T. deferreri</i>	1♂HT, 2♂ 3♀ PTs, JPZ	Morph 1: subspheric	0.71	A	Yes
<i>T. outerelei</i>	1♂PT 1♀, JPZ	Morph 1: subquadrate	0.52	B	Yes
<i>T. quadridentata</i>	1♂HT 1♀PT, MNHNP	Morph 1: subquadrate ^a	0.50	B	Yes
<i>T. belenae</i>	2♂ 1♀ PTs, JPZ	Morph 2: reniform ^a	0.65	C	Yes
<i>T. intermedia</i>	1♂ 1♀ PTs, JPZ	Morph 2: reniform ^a	0.55	C	Yes
<i>T. toribioi</i>	1♂ 1♀ PTs, JPZ	Morph 2: reniform ^a	0.58	C	Yes
<i>T. jeannei</i>	1♂HT 1♂ 1♀ PTs, JPZ	Morph 2: reniform ^a	0.65	C	Yes
<i>T. bullaquensis</i>	1♂HT 1♂ 1♀ PTs, JPZ	Morph 2: reniform ^a	0.60	C	Yes
<i>T. atienzai</i>	1♂HT 1♀PT, JPZ	Morph 2: reniform ^a	0.56	C	Yes
<i>T. estrellae</i>	1♂HT 1♀PT, JPZ	Morph 2: reniform ^a	0.80	C	Yes
<i>T. navarica</i>	1♂ 1♀ PTs, JPZ	Morph 1: subquadrate ^a	1.06	B	Yes
<i>T. laurentii</i>	1♂ 1♀ PTs, JPZ	Morph 1: subspheric	0.58	A	Yes
<i>T. bazi</i>	–	?	?	?	Unconfirmed
<i>T. singularis</i>	1♂ 1♀, JPZ	Morph 1: strongly quadrate	0.61	A	Yes
<i>T. gomesalvesi</i>	2♂ 2♀ PTs, JPZ	Morph 1: subquadrate	0.53	A	Yes
<i>T. elenae</i>	1♂ 2♀ PTs, JPZ	Morph 2: reniform ^a	0.75	C	Unconfirmed
<i>T. crespoi</i>	1♂PT (n° 16100), ARS	Morph 1: subquadrate ^a	0.62	C	Unconfirmed

^aIndicates those species without stridulatory organ. The patterns of sensilla coeloconica are named as in Figure 7. Abbreviations: HT, holotype; PT, paratype; ST, syntype; JPZ, Coll. J.P. Zaballo; ARS, Coll. A.R. Serrano; MNHNP, Muséum national d'Histoire naturelle, Paris; MFNB, Museum für Naturkunde, Berlin.

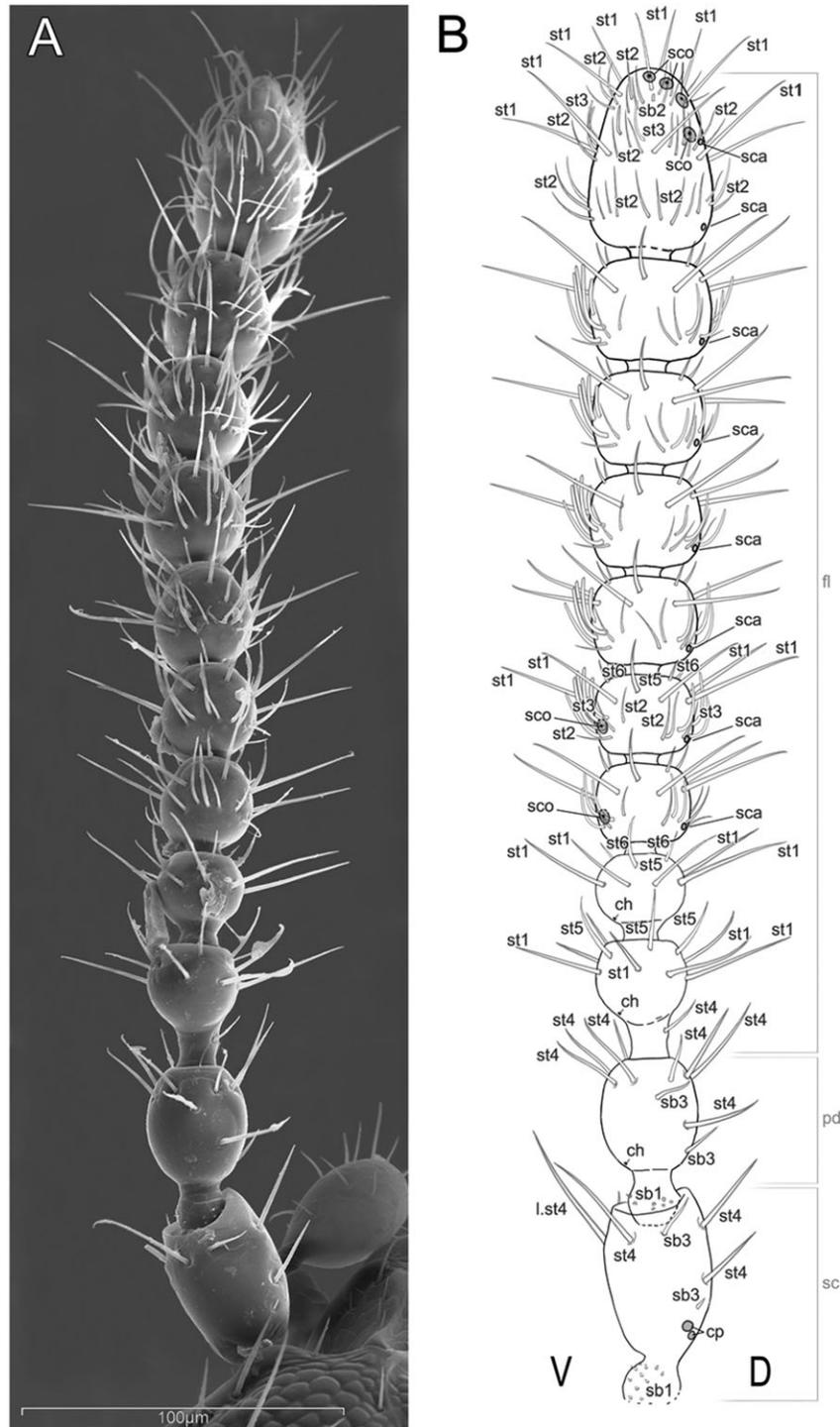


Fig. 1. Left antenna of male *Typhlocharis prima*, as representative of the basic morphology and chaetotaxy pattern for the genus. **A**: SEM photograph in dorso-lateral (scape, pedicel, and third antennomere) and dorsal (fourth to last antennomeres) view. **B**: Schematic diagram of the antenna in lateral view. **D** and **V** indicate dorsal and ventral sides, respectively. Structures mainly studied by light microscopy (**sco**, **sca**, **ch**, **cp**, shaded in grey) are included. Antennomeres 5° to 10° have the same pattern of chaetotaxy, only labeled in antennomere 6°. Abbreviations: **sc**, scape; **pd**, pedicel; **fl**, flagellum; **st1**, **st2**, **st3**, **st4**, **st5**, and **st6**, *sensilla trichoidea* types 1 to 6, respectively; **sb1**, *sensilla basiconica* type 1 (Böhm sensilla); **sb2** and **sb3**, *sensilla basiconica* types 2 and 3; **sco**, *sensilla coeloconica*; **sca**, *sensilla campaniformia*; **ch**, channel-like structures; **cp**, cuticular pores.

different species, distinguishing short-stem forms (~ 0.5–0.7 times the length of antennomere body; Fig. 3B) and long-stem forms (~ 0.7–1.03 times the

length of antennomere body; Fig. 3C). In species like *T. santschii* Normand, 1915 or *T. navarica* Zaballos and Wrase, 1998, elongation of the stem is

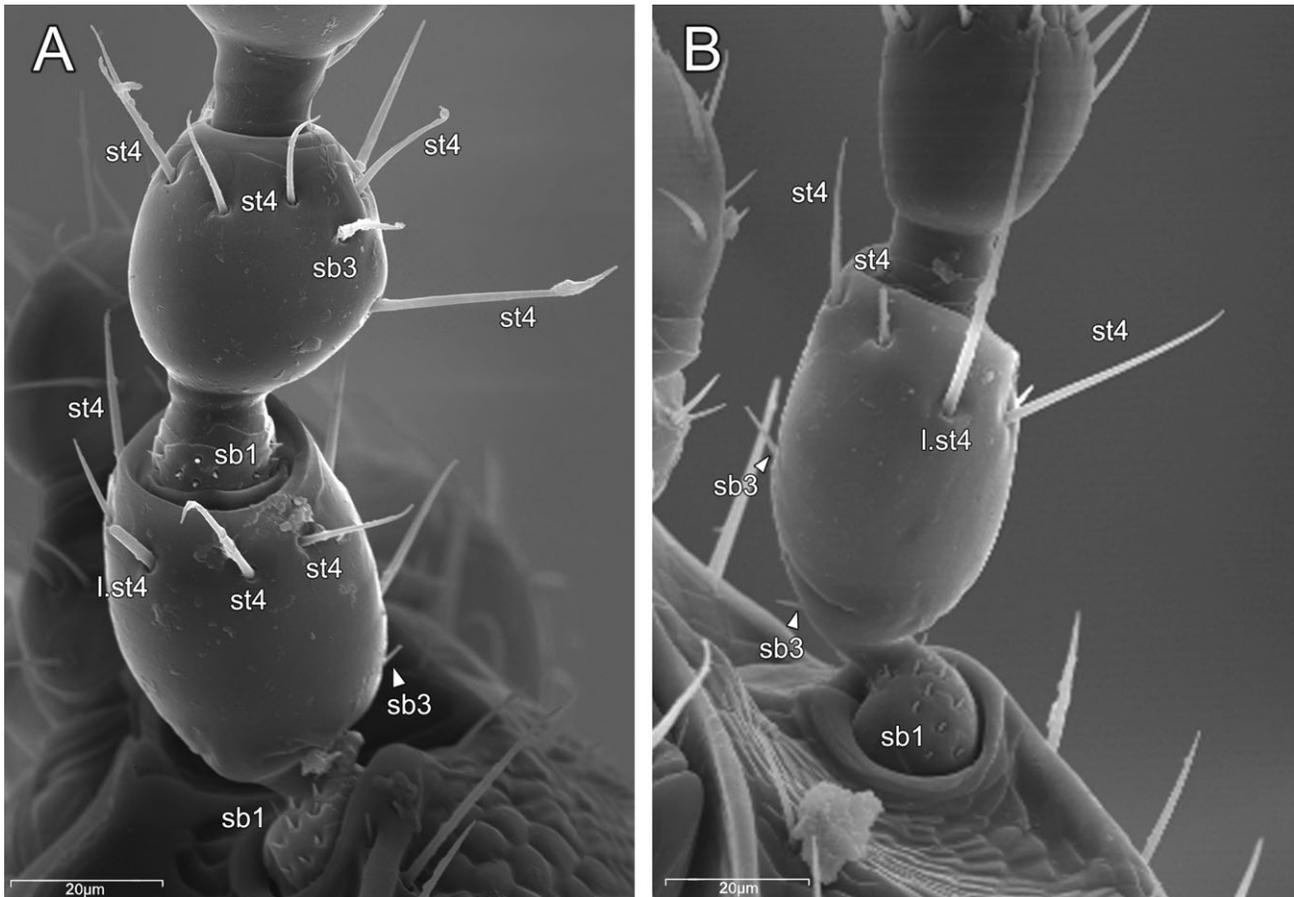


Fig. 2. Scape and pedicel. **A**: Latero-ventral view of scape and pedicel (left antenna, male *Typhlocharis prima*). **B**: Ventral view of scape. Note the spherical basal joint and the presence of long trichoid sensilla (**l.st4**, broken in A) in the ventral side of scape. Abbreviations: **st4**, *sensilla trichodea* type 4; **l.st4**, long *sensilla trichodea* type 4; **sb1**, *sensilla basiconica* type 1 (Böhm sensilla); **sb3**, *sensilla basiconica* type 3.

especially conspicuous (Pérez-González and Zabalos, 2012).

Antennomere 4° is morphologically identical to antennomere 3° (Fig. 1), but always has a short stem (~0.4 times the length of antennomere body).

Antennomeres 5°–10° are similar to each other, slightly compressed laterally and progressively somewhat larger toward distal end of antenna (Figs. 1 and 4). They have significant shape variations between species, with two basic morphologies well differentiated (Fig. 4), affecting the general proportions of the antennae:

- **Morph 1** Rounded antennomeres, including subovoid (Fig. 4A) subspherical (Fig. 4B) and subquadrate (Fig. 4C) morphologies. Species with proportionally longer and slender antennae.
- **Morph 2** Bilobate, reniform antennomeres (Fig. 4D). Species with proportionally shorter and robust antennae.

The specific antennomere morphology of each species is summarized in Table 1.

Last antennomere (11°) is always pyriform or subovoid, compressed laterally, not showing any significant morphological difference between species, except in its breadth, proportional to the rest of antennomeres.

No morphological difference attributable to sexual dimorphism has been observed.

Antennal Chaetotaxy

Types of sensilla. Antennal sensilla can be grouped, by morphology and length, in *sensilla trichodea sensu lato* (six types: **st1–6**), *sensilla basiconica* (three types: **sb1–3**), *sensilla coeloconica* (one type: **sco**) and *sensilla campaniformia* (at least one type: **sca**).

Sensilla trichodea: Type 1 (**st1**) are long and straight, hair-like setae. They point outwards and appear in all the flagellomeres (Figs. 1, 5A,B,D, 6A,B, 9B). Type 2 (**st2**) are medium sized, slightly curved, thin sensilla, with filiform apex, distributed in antennomeres 5° to 11° (Figs. 1, 5A,B,D,E, 6A,B,D, and 9B). Type 3 (**st3**) are medium sized,

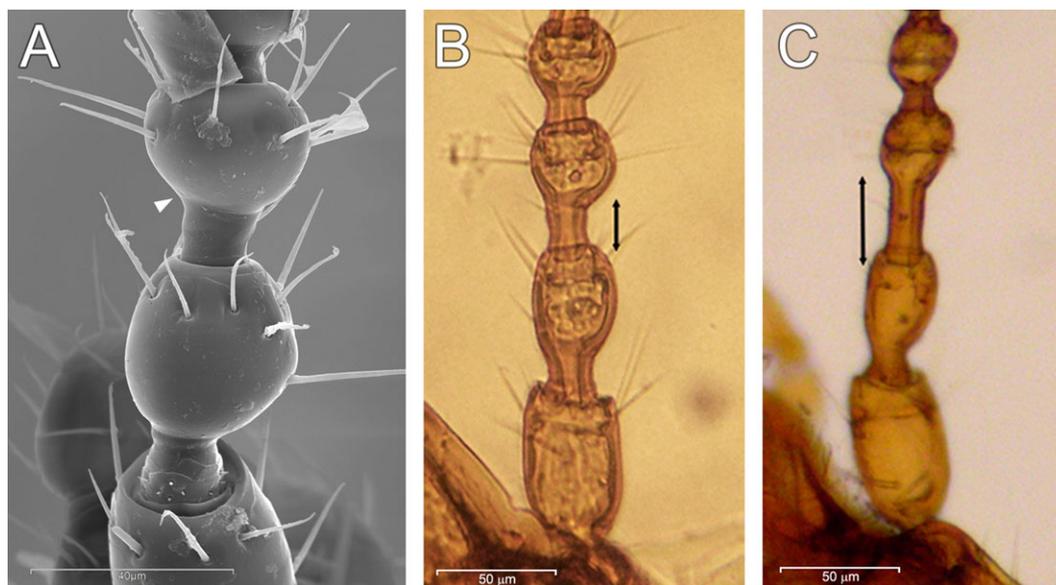


Fig. 3. Third antennomere. **A**: SEM photograph of the third antennomere in male *Typhlocharis prima* (left antenna, lateral view). White arrow indicates the presence of a channel-like structure. **B–C**: Light microscopy photographs showing the variation range of the third antennomere; **B**: Short-stem form (*T. armata*). **C**: Long-stem form (*T. santschii*).

thick sensilla, with blunt apex and strongly bent at the base (Figs. 1, 5A,B,D,E, 6A,B, and 9B). In species of *Typhlocharis* with reniform flagellomeres (morph 2), these sensilla are thicker and their morphologic differentiation from the other types of sensilla is more pronounced. **St3** are present in antennomeres 5° to 11°. Type 4 (**st4**) resembles **st1**, but are more robust, ranging from medium sized to long sensilla, and only appears in scape, pedicel and the stem of first flagellomere (Figs. 1, 2A,B and 6E,G). Type 5 (**st5**) are medium to long, curved, sabre-like sensilla (Figs. 1 and 6A,B), present in all the flagellomeres. These sensilla are thicker and shorter in species with reniform flagellomeres and differ from **st2** in the shape of the curve and a slightly lateral compression. Type 6 (**st6**) are always short, thin, and straight, located only in the distal surface of antennomeres 4° to 10° (Figs. 1 and 6A,B).

Sensilla basiconica: Type 1 (**sb1**) appears in the stem of scape and pedicel. They are very short conic structures, regarded as Böhm sensilla (Figs. 1, 2, and 6F). A second type (**sb2**) of very short, strongly bent sensilla is observed in the 11° antennomere (Figs. 1, 5A,B, and 6C,D). They resemble a miniaturized version of **st3** sensilla, and are very rare. Type 3 (**sb3**) includes short or very short conic or hair-like sensilla, located in the dorsal surface of scape and pedicel and occasionally in antennomere 3° (Figs. 1, 2, and 6E,F). The number and distribution of these sensilla varies randomly within the genus.

Sensilla coeloconica (**sco**) are distinguishable as crater-like, small pit structures (Figs. 1, 5, 6C,H, and 9B,C). The tip of small sensillum is visible

inside the orifice (Fig. 5E). They appear in antennomeres 5°, 6°, and 11°.

Structures resembling *sensilla campaniformia* (**sca**) are visible by light microscopy as several spots on the cuticular surface of the antennomeres, near the base of each one (Figs. 1, 5C, and 10D), from antennomere 5° to 11°. Two similar structures appear at the base of scape (Figs. 1 and 10A). Scanning electron microscopy, however, only allowed confirmation of the identity of these structures as true **sca** in antennomeres 10° and 11° (Figs. 5B,E and 6A,I). The appearance of confirmed **sca** under light microscopy suggests all the other structures are of the same type, but their identification remains uncertain. The structures in the scape may correspond to cuticular pores (**cp**). The distribution pattern of these structures is virtually constant in the entire genus.

Distribution of sensilla. Scape and pedicel shows a similar chaetotaxy, sharing both a pattern of Böhm sensilla (**sb1**) in the stem, one robust **st4**, located dorsally, generally accompanied by one or two (rarely more) **sb3**, and a distal “ring” of **st4**. In the scape, one of these distal **st4** (located ventrally) stands out as specially long, approx. twice the length of the others. There are also two circular unidentified structures dorsally near the base of the scape, resembling **sca** under light microscopy. The pedicel has a small cuticular channel-like structure (**ch**) ventrally near the base of the antennomere body (Figs. 1 and 10B).

Antennomere 3° has a medium sized **st4** dorsally, in the stem (absent in some species). The body of the antennomere presents a medial “ring” of **st1** and a subapical “ring” of **st5**. Ventrally,

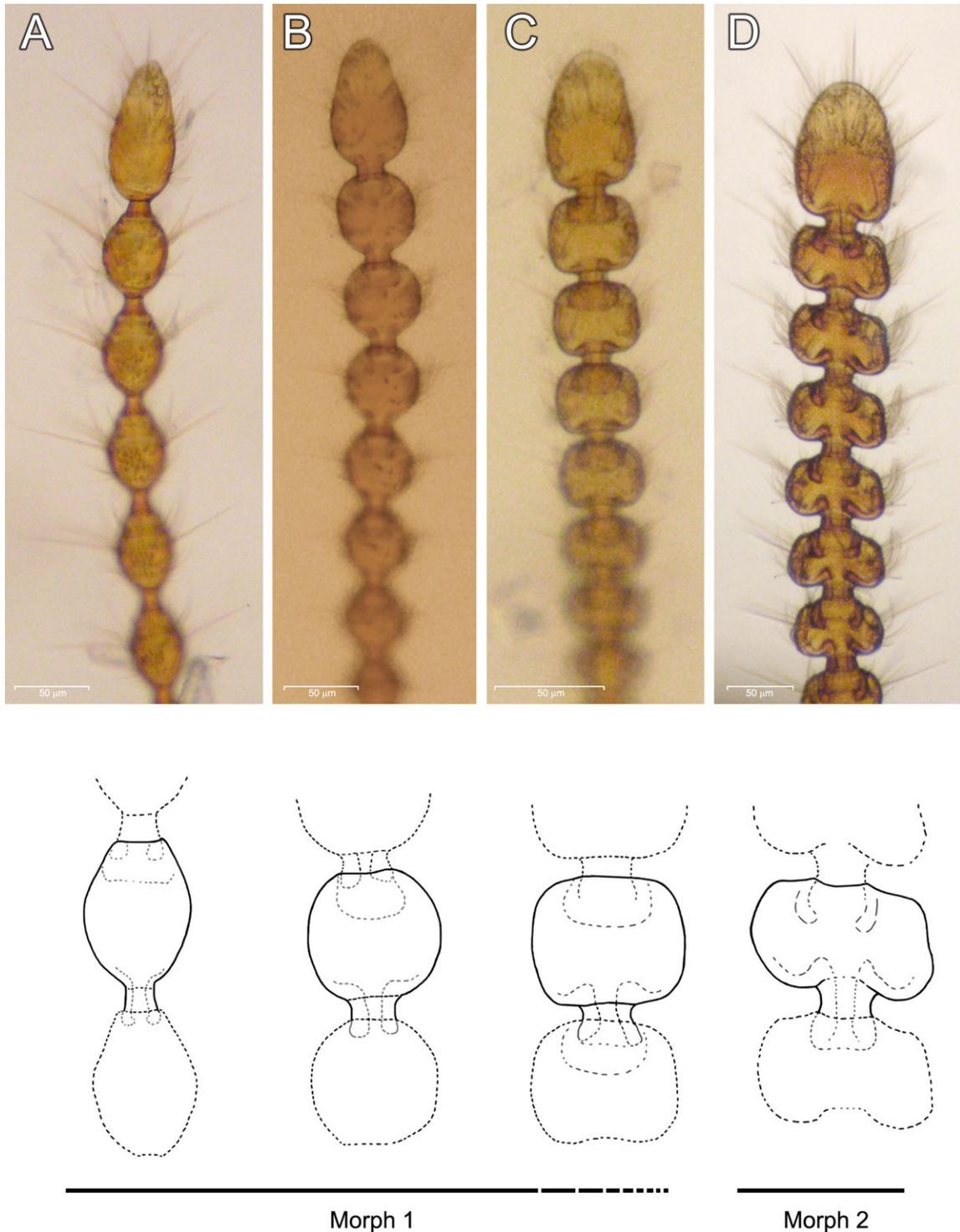


Fig. 4. Morphological differences in flagellomeres. **A–D**: Light microscopy photographs of flagellum (right antenna, lateral view) and schematic diagrams of antennomere 9° , showing the morphological variations: **Morph 1**, rounded shapes: **A**: Subovoid (*Typhlocharis algarvensis*); **B**: subspheric (*T. sarria*); **C**: subquadrate (*T. crespoi*). **Morph 2**: **D**: reniform (*T. farinosae*). Note that morph 1 covers a progressive transition to the exaggerated condition observed in morph 2.

there is the same type of channel-like structure (**ch**) as described in the pedicel (Figs. 1, 3A, and 10C).

Antennomere 4° shares the same chaetotaxy pattern as 3° , except there are no sensilla in the

stem, and the subapical “ring” consists of one lateral pair of **st5** and one or two **st6** in the dorsal and ventral apical surface. The ventral channel-like structure (**ch**) is present.

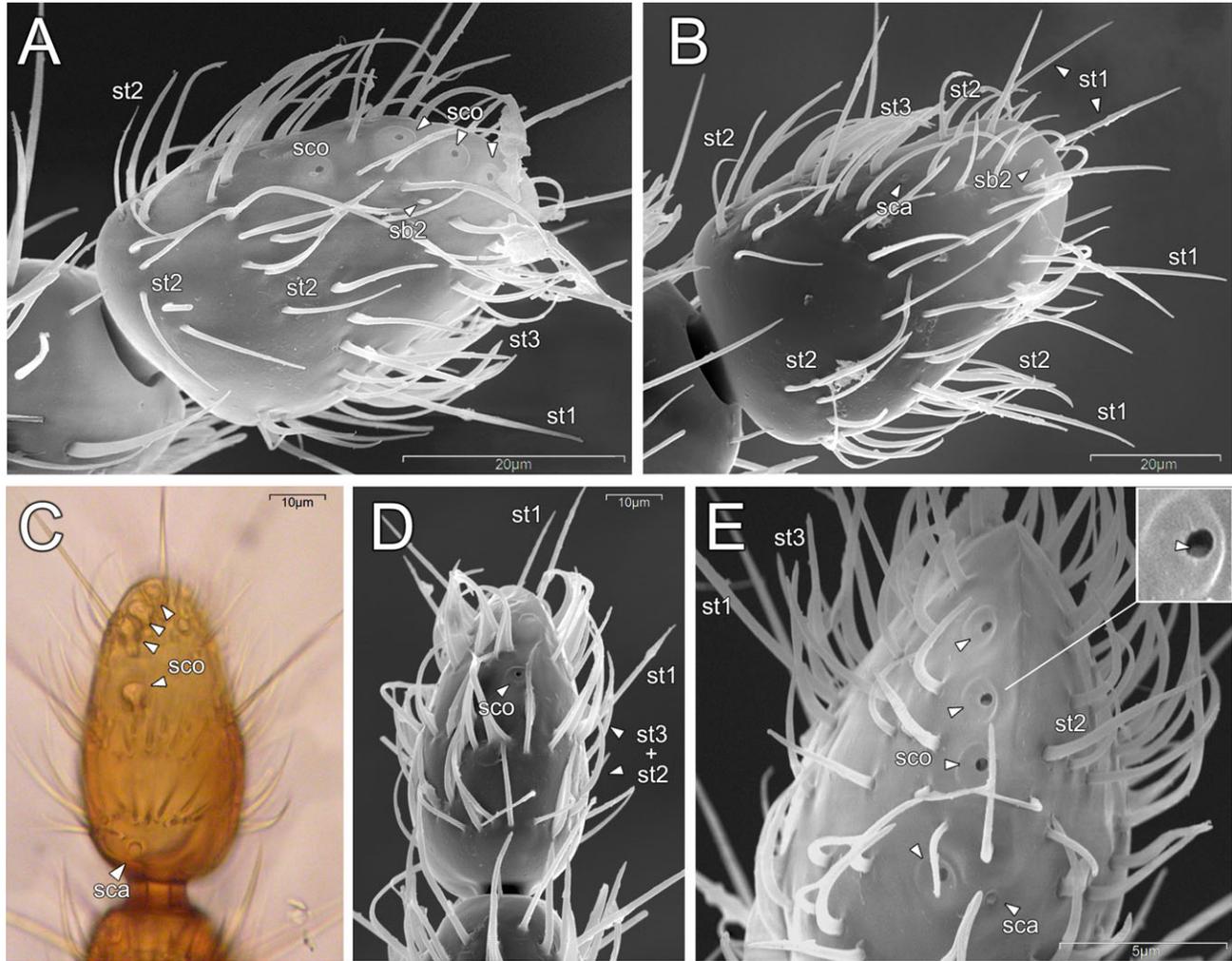


Fig. 5. Last antennomere (11°). **A**: Medial view (left antenna, male *T. prima*). **B**: Lateral view (right antenna, female *T. prima*). **C**: Dorso-medial view, light microscopy (left antenna, female *T. quarta*). **D**: Dorsal view (right antenna, male *T. prima*). **E**: Dorso-apical view (right antenna, male *T. prima*); upper right corner: detail of the orifice, white arrow points to the inner sensilla. Abbreviations: **st1**, **st2**, and **st3**, *sensilla trichoidea* types 1 to 3, respectively; **sb2**, *sensilla basiconica* type 2; **sco**, *sensilla coeloconica*; **sca**, *sensilla campaniformia*. Note the characteristic “mushroom” shape of **sco** in 5C (light microscopy image).

Antennomeres 5° to 10° shares all the same pattern, consisting of a basal “ring” of interspersed **st3** and **st2**, a medial “ring” of very long **st1** and a subapical “ring” with two **st5** (one lateral, one medial) and two pairs (one pair dorsal, one pair ventral) of **st6** (Figs. 1, 6A,B, and 8). There is a dorsal circular structure in each one, identifiable as **sca** (confirmed in the 10° antennomere). **St3** are much more abundant and densely grouped in the ventral side, especially in those species with reniform antennomeres (morph 2). The basal “ring” of **st2** and **st3** is strongly affected by the shape of antennomere (Fig. 8), distorted in species with reniform antennomeres (morph 2). Antennomeres 5° and 6° have one *sensillum coeloconicum* (**sco**) located ventrally (unconfirmed in some of the studied species; Figs. 1 and 9).

The last antennomere (11°) presents the highest diversity and abundance of sensilla, distributed in

three “rings”: the first, basal ring, composed by **st2** and **st3**, the second, medial ring, formed by **st1**, **st2**, and **st3** (**st1** well differentiated by their greater length) and the third, apical ring, also formed by **st1**, **st2**, and **st3** (Figs. 1 and 5) with some scattered and rare **sb2**. Two or three scarce *sensilla campaniformia* (**sca**) appears in the dorso-lateral and mid-dorsal regions of antennomere body (Figs. 1 and 5B,E). There are *sensilla coeloconica* (**sco**) in the dorso-medial region of antennomere, following a distribution pattern which varies between species (Figs. 1, 5 and 7). In practically all the species, **sco** are apparently arranged in two groups: “anterior”, with one to six sensilla; and “posterior”, with only one isolated sensillum. The most common pattern observed consist of three “anterior” **sco** in a row, followed by one isolated “posterior” **sco**, more or less separated (Fig. 7A). The patterns observed in *T. fancelloi* Magrini,

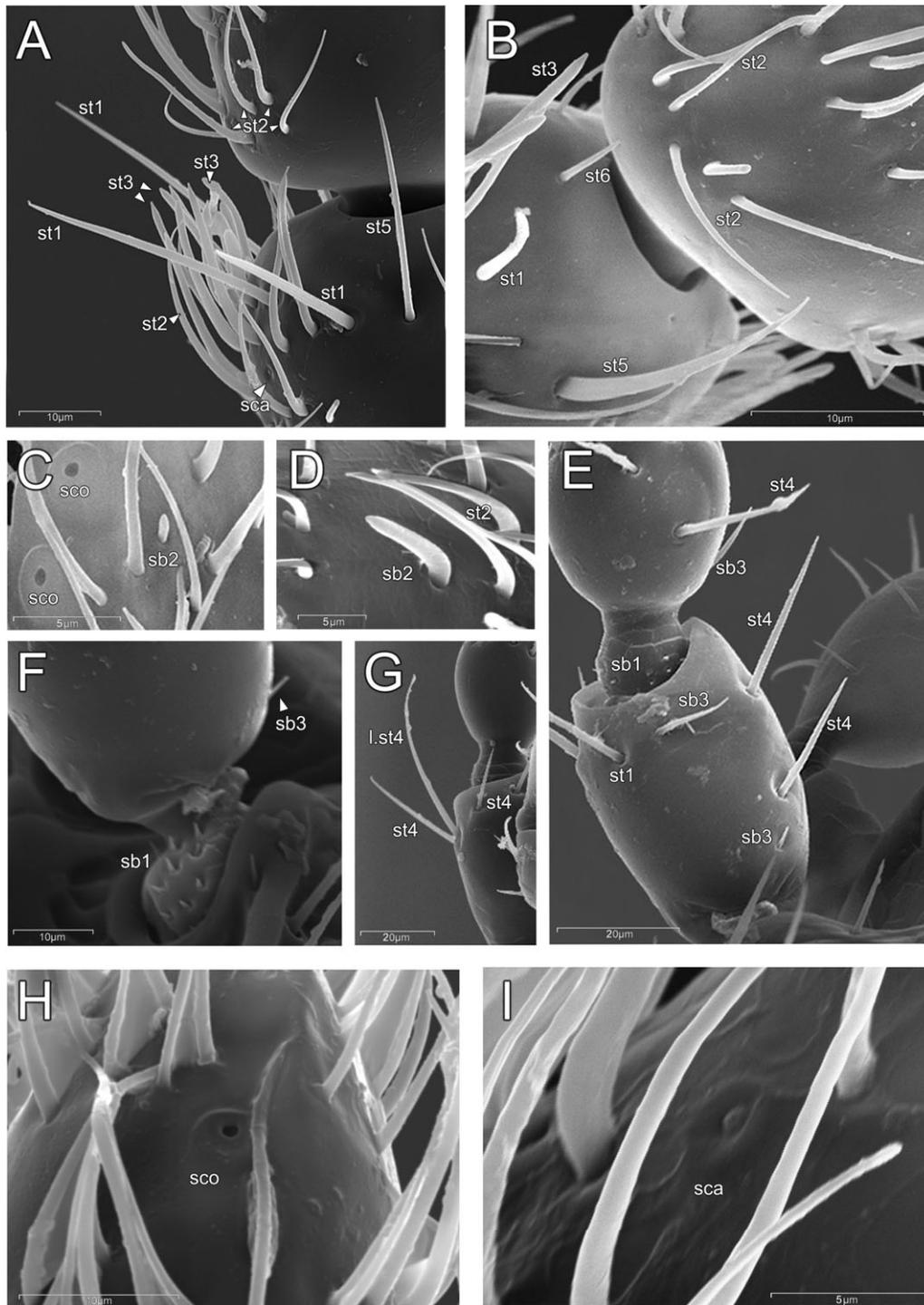


Fig. 6. Antennal sensilla in *Typhlocharis prima*. **A-D**: Antennomeres 3°-11° (flagellomeres). **E-G**: Scape and pedicel. **H-I**: Antennomere 11°. **A**: Lateral view of antennomere 10°. **B**: Medial view of antennomere 10°. Note the differences between thin, hair-like sensilla (**st2**) and thick, blunt apex sensilla (**st3**) (white arrows) and the sabre-like aspect of **st5**. **C,D**: Details of the basiconic sensilla (**sb2**) in antennomere 11°. **E**: Dorso-lateral view of the scape. **F**: Scape base. **G**: Ventro-lateral view of scape. Note the presence of extraordinarily long trichoid sensilla (**l.st4**). **H**: Detail of a coeloconic sensillum in antennomere 11°. **I**: Detail of a campaniform sensillum in antennomere 11°. Abbreviations: **st1**, **st2**, **st3**, **st4**, **st5**, and **st6**, *sensilla trichoidea* types 1 to 6, respectively; **l.st4**, long *sensilla trichoidea* type 4; **sb1**, *sensilla basiconica* type 1 (Böhm sensilla); **sb2** and **sb3**, *sensilla basiconica* types 2 and 3; **sco**, *sensilla coeloconica*; **sca**, *sensilla campaniformia*.

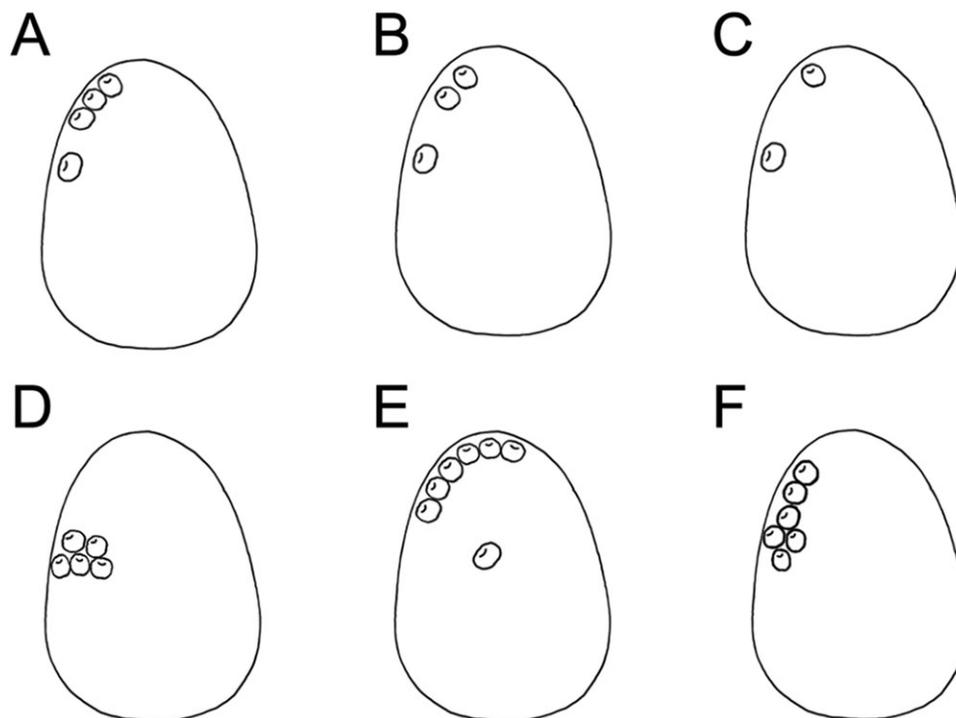


Fig. 7. Distribution patterns of *sensilla coeloconica* (antennomere 11°, medial view) within genus *Typhlocharis*. **A**: Group of three sensilla plus isolated sensillum, in row (e.g., *T. armata*). **B**: Group of two sensilla plus isolated sensillum, in row (e.g., *T. rochapitei*). **C**: Two isolated sensilla, in row (e.g., *T. carpetana*). **D**: Five “bunched” sensilla, (*T. fancelloi*). **E**: Group of six sensilla, in row, plus isolated medial sensillum, (*T. carinata*). **F**: Six sensilla grouped in “inverted t” shape (*T. algarvensis*).

2000 (five **sco**, “bunched”) and *T. algarvensis* Coiffait, 1971 (six **sco** arranged in “inverted t” shape) are exceptional (Fig. 7D,F, respectively).

DISCUSSION

Antennae have not received much attention when describing and characterizing Anillini features. In the morphological descriptions of genus *Typhlocharis*, the antennae have been repeatedly described as “moniliform, without special features” (e.g., Serrano and Aguiar, 2008;; Andújar et al., 2010; Ortuño and Gilgado, 2011; Pérez-González and Zaballos, 2012), implying they are relatively similar in all the species. One of the aims in this work has been to question this information and try to evaluate the taxonomic potential of those antennal features with an observed pattern of variation between species.

Shape of the Flagellomeres

The morphological differences of antennomeres 5°-10° are remarkable. The observed morphologies (Fig. 4) follows a progressive gradient from ovoid to reniform, lobate shapes, passing through intermediate subspherical and subquadrate forms.

These differences could respond to phylogenetic or functional factors. Jeanne (1973) postulated

that a morphological gradient can be distinguished within *Typhlocharis*: the larger forms present a high number of setae (seven or eight) in the umbilicate series of elytra and the smaller forms usually present reduced umbilicate series (four to six setae) and toothed posterior margin of elytra. Such differences were attributed as a result of increasing specialization to the strictly endogean and hypogean environments (Zaballos, 1989), passing by a progressive body size reduction, reflected in the shortening of elytra (appearance of the apical teeth) and reduction of the umbilicate series. This hypothesis has been partially rejected in its strict sense, given that the pattern of loss of setae and appearance of apical teeth in elytra are not directly correlated to reduction of body size, as demonstrated by the *baetica* group (Zaballos and Banda, 2001; Pérez-González and Zaballos, 2013), but the main idea is still coherent to the available data.

The morphology of flagellomeres (Table 1) seems to fit the hypotheses of Jeanne (1973) and Zaballos (1989): larger species with high number of umbilicate setae always have rounded, subovoid or subspherical flagellomeres (morph 1), and smaller species with reduced umbilicate series have reniform flagellomeres (morph 2). Subquadrate flagellomeres can be interpreted as transitional forms between these morphs. Assuming the interpreta-

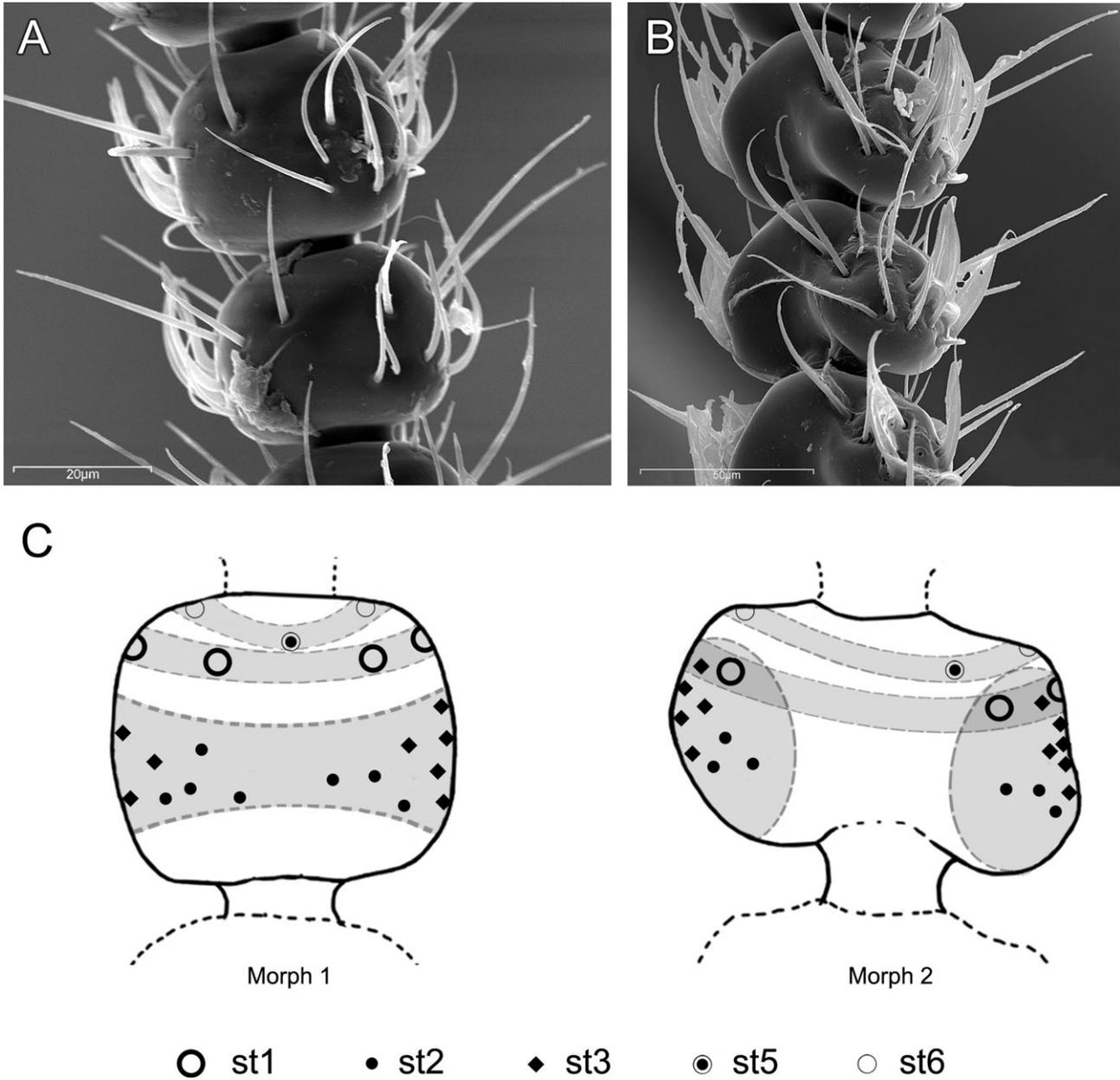


Fig. 8. Flagellomere chaetotaxy associated to the two main morphologies. **A:** Morph 1, dorso-lateral view of antennomeres 6° and 7° in *Typhlocharis prima*. **B:** Morph 2, ventro-lateral view of antennomeres 6° and 7° in *T. farinosae*. **C:** Schematic diagrams of sensilla distribution in both morphs. Note the distortion of the “rings” (shaded in grey) caused by displacement of sensilla toward dorsal and ventral sides of the flagellomere in morph 2. Abbreviations: **st1**, **st2**, **st3**, **st5**, and **st6**, *sensilla trichoidea* types 1 to 6, respectively.

tion of Zaballos (1989) about Jeanne’s hypothesis, the presence of reniform antennomeres with dorsal and ventral distribution of **st2** and **st3** might be a specific adaptation of those species more strictly endogean.

The comparison of the morphology of antennomeres with other characters studied for the genus (see Table 1 in Pérez-González and Zaballos, 2012) suggest this character can be added to the defini-

tion of morphological trends within the genus. Also, some of the antennal characters (Table 1) may reflect phylogenetic signal, especially the shape of flagellomeres and the pattern of *sensilla coeloconica* in the last antennomere, which seems to be correlated. Species with reniform flagellomeres tend to have certain pattern of *sensilla coeloconica* (Fig. 7C). Other characters, like the presence of *sensilla coeloconica* in antennomeres 5°

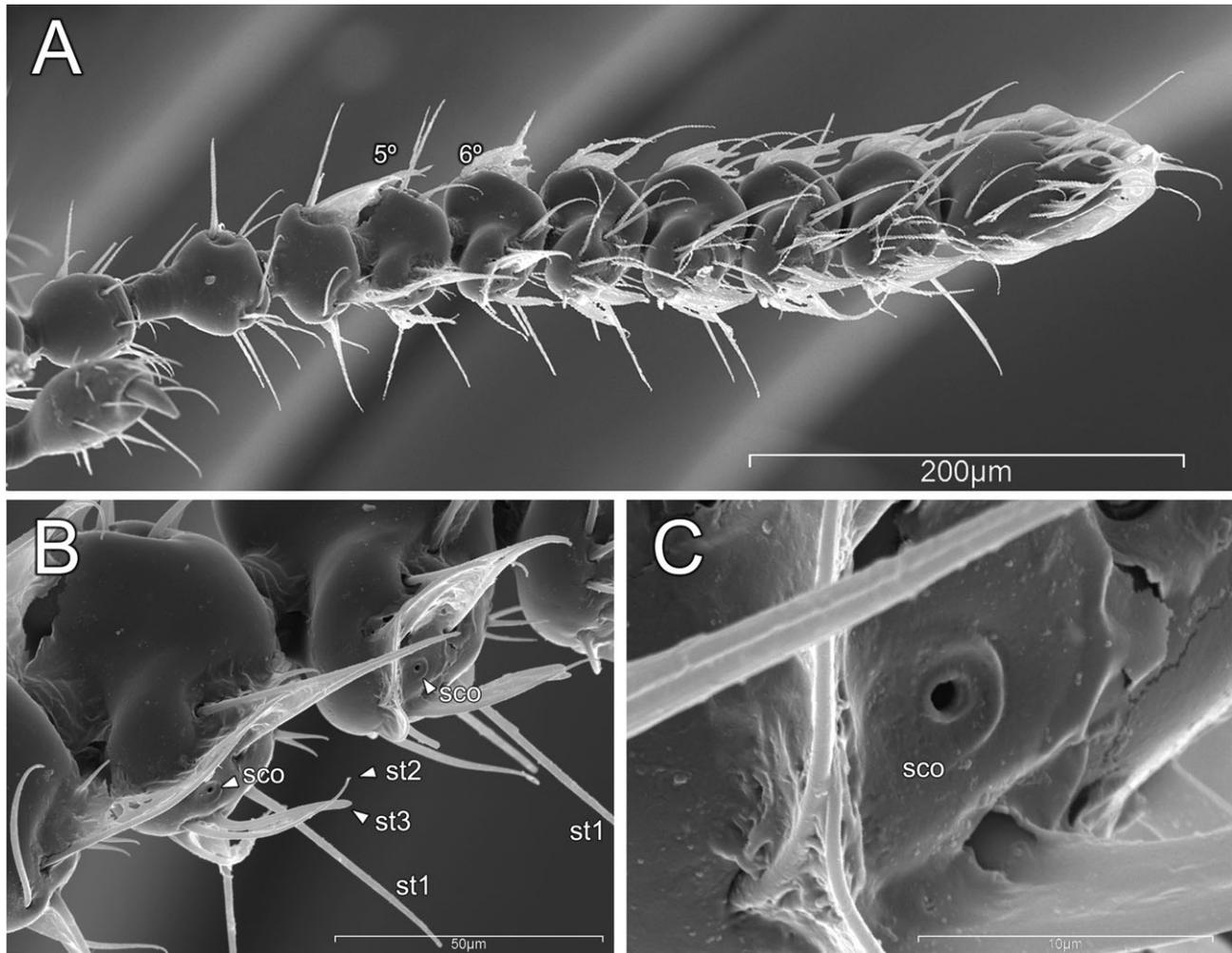


Fig. 9. Ventral *sensilla coeloconica* in antennomeres 5° and 6°. **A**: Flagellum of male *Typhlocharis farinosae* (ventro-medial view). **B**: Detail of the ventral side of antennomeres 5° and 6°. **C**: Detail of the *sensillum coeloconicum* in antennomere 6°. Abbreviations: **st1**, **st2**, and **st3**, *sensilla trichoidea* types 1 to 3, respectively; **sco**, *sensilla coeloconica*.

and 6° turned out to be virtually identical in the whole genus, thus they are not useful to discriminate relationships between species.

Distribution and Diversity of Trichoid and Basiconic Sensilla

The sensilla found in *Typhlocharis* are similar to those described for other Carabidae (Daly and Ryan, 1979; Kim and Yamakasi, 1996; Merivee et al., 2000, 2001, 2002, Giglio et al., 2008). Ploomi et al. (2003) summarize the data given by Merivee et al. (2000, 2001, 2002) providing a comparative basis between the antennal sensilla of three carabids, including two Trechinae. The data obtained in *Typhlocharis* is compared to the nomenclature of setae described in this work:

- **St1** resemble *sensilla chaetica* type 2 as defined by Ploomi et al. (2003). **St2** are probably equiva-

lent to *sensilla chaetica* type 1 by Ploomi et al. (2003) and are the most abundant. These setae have been regarded as mechanoreceptors (**st1**, **st2**) and contact chemoreceptors (**st1**) (Ploomi et al., 2003; Merivee et al., 2000, 2001, 2002).

- **St2** often appears interspersed with **st3** in *Typhlocharis* and in some species is difficult to tell both types apart, given the variation of **st3** thickness and the density of **st2** and **st3** aggregations. However, they are distinguishable by the thick, blunt apex of **st3** and the thin, filiform apex of **st2**. **St3** resemble *sensilla trichodea* type 2 and *sensilla basiconica* type 1 *sensu* Ploomi et al. (2003) and correspond to the “finger-shaped” setae referred by Ortuño and Sendra (2010). **St3** may be classified as *sensilla basiconica*, but differentiation from *sensilla trichodea* based only in the external morphology is extremely difficult. They are considered olfactory structures and they have been suggested to be

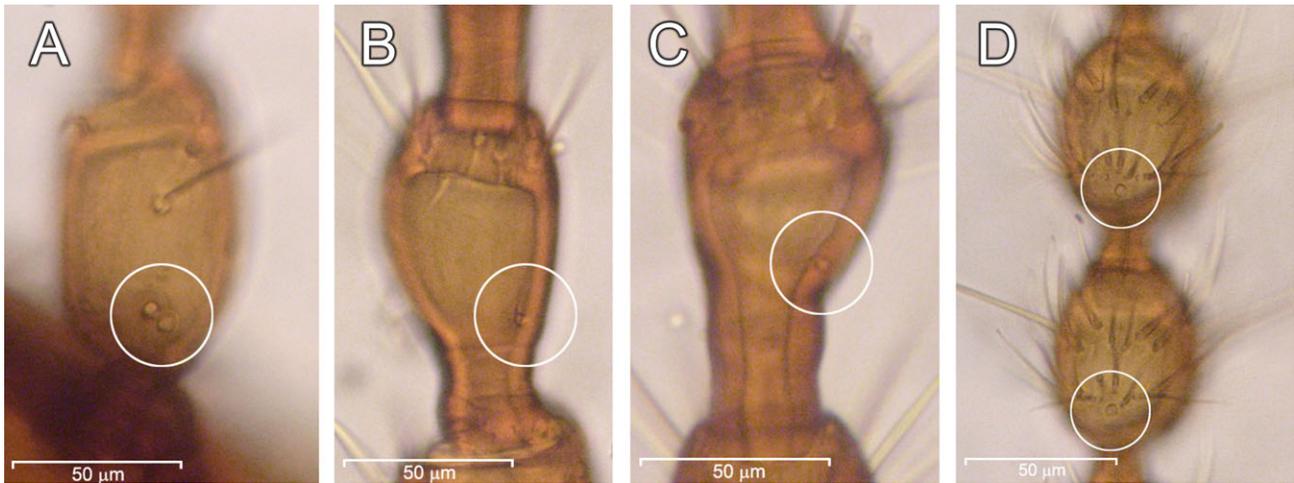


Fig. 10. Structures undetermined by SEM, but visible by light microscopy (*Typhlocharis quarta*, female). **A**: Dorsal circular structures in the base of scape. **B**: Ventral channel-like structure near the base of pedicel body. **C**: Ventral channel-like structure near the base of third antennomere body. **D**: Dorsal circular structures near the base of flagellomeres body, confirmed as *sensilla campaniformia*.

aggregation pheromone receptors (Merivee et al., 2000, 2001, 2002; Ploomi et al., 2003).

- **St4** are very similar to the *sensilla chaetica* type 3 *sensu* Ploomi et al. (2003). They are probably mechanoreceptors. The long **st4** observed in the ventral side of the scape is also present in *Bembidion lampros* (Herbst, 1784), *B. properans* Stephens, 1827 and *Platynus dorsalis* (Pontoppidan, 1763); regarded as *sensilla chaetica* type 3 or “long *sensilla chaetica*” by Ploomi et al. (2003). **St5** and **st6** does not have a clear equivalent. Their structure and location (apical region of the flagellomeres) suggest a mechanoreceptive function (Zacharuk, 1985).

The diversity of *sensilla basiconica* is relatively low in *Typhlocharis*. Only three different types were found, in contrast to the at least six types described for *Bembidion lampros*, *B. properans* and *Platynus dorsalis*. All the types present in *Typhlocharis* are probably equivalent to one of the types defined in Ploomi et al. (2003). **Sb1** (Böhm sensilla) are found in the base of scape and pedicel in many beetles and they probably function in mechanoreception or proprioception (Merivee et al., 2000, 2002). **Sb2** are very rare. Only one or two sensilla of this type are found in the last antennomere. They correspond to *sensilla basiconica* types 1 or 2 as defined by Ploomi et al. (2003) and are probably olfactory structures. **Sb3** are small bristles, variable in size and number, resembling miniaturized trichoid sensilla. They often accompany **st4** in scape and pedicel and correspond with *sensilla basiconica* type 5 *sensu* Ploomi et al. (2003), probably mechanoreceptors.

The disposition of trichoid sensilla is very constant within the genus, but the layout of the various “rings” of sensilla in every antennomere depends on

its shape (Fig. 8). In species with reniform antennomeres (morph 2), the “ring” of **st2** and **st3** is gathered in the dorsal and ventral regions, more abundant and densely grouped in the latter. In species with rounded or subquadrate antennomeres (morph 1), the “rings” are more homogeneously distributed on the entire antennomere surface, although the ventral region is also the most densely covered.

The higher density of ventral sensilla in the antennomeres is probably related to the functionality of the antennae and peculiarities of search behavior (Merivee et al., 2002). **St3**, considered olfactory, are the most abundant type in these areas and are especially thick and dense in species with reniform flagellomeres (morph 2). This may suggest a more important role for olfaction and chemoreception in these species.

There is also a clear correlation between flagellomere morphology and another cephalic structure, that is, the stridulatory organ (*pars stridens*). The latter is widespread within the genus but absent precisely in that species with reniform flagellomeres (Table 1). This could imply differences in the communication mechanisms or behavior of the genus, from sound production to pheromone reception as suggested by Zaballos and Pérez-González (2011a). The use of aggregation pheromones is known in other carabids (Merivee et al., 2000) and it is possible for *Typhlocharis*, which may also explain why some species are sometimes captured in large numbers (Pérez-González and Zaballos, 2013).

***Sensilla campaniformia* and other Cuticular Structures**

Sensilla campaniformia are regarded as mechanosensory structures (Zacharuk, 1985). Merivee

et al. (2002) describe the presence of two large pores near a cuticular depression, dorsally, in the base of scape in *Bembidion properans*. The location of these pores corresponds exactly with the location of the “two circular structures” present in *Typhlocharis* and explained as possible *sensilla campaniformia* (Fig. 10A). None of the SEM micrographs reveals the true identity of this structure in *Typhlocharis*, but the location suggests both structures are homologous. Also, the “channel-like” structures reported in pedicel and antennomeres 3° and 4° of *Typhlocharis* (Fig. 10B,C) probably correspond to cuticular pores as described by Merivee et al. (2002; Fig. 3A).

Distribution and Patterns of the Coeloconic Sensilla

In Anillini with available information on the presence and distribution of *sensilla coeloconica* in the last antennomere, like *Aphaenotyphlus alegrei* Español and Comas, 1985 and *Microtyphlus infernalis* Ortuño and Sendra, 2010 (Ortuño and Sendra, 2007, 2010), these sensilla are apparently arranged in two groups, as “L” or “cross” shaped aggregations. This type of aggregation is observed in *Typhlocharis*, but in the majority of the species the *sensilla coeloconica* are arranged in a row with posterior single sensilla (Fig. 7, Table 1). Only two studied species (*T. fancelloi* Magrini, 2000 and *T. algarvensis* Coiffait, 1971) do not show a row pattern for these sensilla. *T. fancelloi* Magrini, 2000 have five “bunched” sensilla (Fig. 7D). *T. algarvensis* Coiffait, 1971, with six sensilla arranged in “inverted t” shape (Fig. 7F), resembles the pattern of *Aphaenotyphlus* and *Microtyphlus*, but there is no noticeable separation between sensilla. Also, there is certain degree of individual variation; some specimens present supernumerary, infranumerary, or displaced sensilla, altering the described main patterns. These rare alterations were observed affecting one (asymmetric pattern) or both antennae.

In *Microtyphlus infernalis* Ortuño and Sendra, 2010 aggregations of several *sensilla coeloconica* are described in distal antennomeres 9° and 10°. *Typhlocharis* have a different pattern: distal antennomeres 9° and 10° lack any *sensilla coeloconica*, but middle antennomeres 5° and 6° have one *sensillum coeloconicum* each one, in the ventral side (Fig. 9).

These sensilla probably function as thermohygro- and chemoreceptors (Zacharuk, 1985; Ploomi et al., 2003).

Differences in the Stem of Third Antennomere

There are considerable differences in the length of the stem of antennomere 3°. In antennae with long-stem antennomere 3°, there is a noticeable

separation from the flagellomeres group respect to the scape and pedicel. The list of species with long/short stem is given in Table 1.

It is uncertain if the elongation of the stem represents phylogenetic affinities. There is no correlation between elongation of the stem and the chaetotaxy of the third antennomere, as there are no significant differences in the chaetotaxy of this antennomere within the genus. The species with longest stems (*T. santschii* Normand, 1915; *T. navarica* Zaballos and Wrase, 1998; *T. peregrina* Zaballos and Wrase, 1998 and *T. monastica* Zaballos and Wrase, 1998) (Pérez-González and Zaballos, 2012) share certain morphological features that suggest close affinities between them, but the differences they have and the fact that some other species have moderately elongated stems, intermediate between short-stem and long-stem forms, does not allow to discard the multiple origin of this feature.

NOTE ON THE METHODOLOGY

Finally, it should be noted that distribution and patterns of antennal structures, properly identified with scanning electron microscopy, can be observed and adequately studied by traditional light microscopy. Sometimes, structures such as *sensilla campaniformia* are even easier to detect by light microscopy, given the internal structure visible by transparency (Fig. 10). This supposes a subsequent saving of time and specimens available for study in taxa which are rarely represented by large series.

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