A revision of the spring-tail genus Vesicephalus Richards (Collembola, Symphypleona, Sminthurinae)

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ABSTRACT

A detailed morphological study of the collembolan genus Vesicephalus Richards in Delamare Deboutteville & Massoud, 1964 is presented, with the redescription of known species on the basis of new scanning electron microscopy observations. Vesicephalus is a rare genus found in North America, Spain (Europe) and Russia, having the unique characteristic of a pair of interocular vesicles with demonstrated photoreception function. This feature may be responsible for habitat restriction within the species range. The possible function of this photoreceptor is high sensitivity to light, which permits these animals to live in a dark environment. A key to the known five species is presented, together with chaetotaxic illustrations.

INTRODUCTION

In 1956, Richards described the genus Vesicephalus in his unpublished PhD dissertation. Delamare Deboutteville & Massoud (1964) validly published the name in a revision of the genus and placed it in the subfamily Vesicephalinae Richards in Delamare Deboutteville & Massoud, 1964.

The genus currently includes Vesicephalus longisetis (Guthrie, 1903) (Fig. 1a), Vesicephalus occidentalis (Mills, 1935) (Fig. 1b) and Vesicephalus crossleyi Snider, 1985 from North America, Vesicephalus europaeus Ardanaz & Pozo, 1985 (Fig. 1c, d) from the northern Iberian Peninsula and Vesicephalus bellingeri Bretfeld, 2002 (Fig. 1e, f) from eastern Russia (Fig. 2). Richards (1968) listed another, undescribed American species (Vesicephalus sp.), that we have been unable to find, and Richards gave no information about its distribution.

Whilst taking samples for the project 'Fauna Iberica', live specimens of V. europaeus were captured. This species had been described in 1985 from only three specimens captured in pitfall traps from northern Spain. Our new specimens allowed an in-depth

morphological study by optical microscopy and scanning electron microscopy (SEM), and enabled a more detailed redescription of the species. This new description, which modified the original, led us to believe that descriptions of the North American species could also be incomplete. Therefore, we examined type material from different museums by light microscopy. In the case of V. crossleyi, from the Department of Entomology at Michigan State University, we also prepared a male paratype for SEM observation.

MATERIALS AND METHODS

Material is deposited in the following collections:
MSU, Michigan State University, Zoology Department; UMN, University of Minnesota, Department of Entomology;
INHS, Illinois Natural History Survey, University of Illinois;
MZNA, Museo de Zoología, Universidad de Navarra, Spain;
Bretfeld personal collection, Zoological Institute, University of Kiel. Olshausenstrasse 40, D-24098 Kiel, Germany.

Specimens of V. europaeus selected for this study were separated from leaf litter using Berlese–Tullgren funnels. Preparation for SEM was performed using a 2 : 2 : 1 mixture of methanol, acetic acid and water for fixation (Saito & Osakabe, 1992), critical point drying with CO2 and gold coating to a thickness of 16 nm (using an Emitech K550, Emitech Ltd., Ashford, Kent, U.K.). Microscopic observations were made with a Zeiss DSM 940 A (Zeiss, Oberkochen, Germany).

The chaetotactic notation used follows Baquero et al. (2003) for the head, Betsch & Bretfeld (1991) for the abdomen, Bretfeld (2002) for the small abdomen and Nayrolles (1987) for the tibiotarsi.

TAXONOMY OF THE GENUS VESICEPHALUS RICHARDS IN DELAMARE DEBOUTTEVILLE & MASSOUD, 1964

Vesicephalus Richards, 1956: 190 [unpublished].
Vesicephalus: Delamare Deboutteville & Massoud 1964: 75.
Vesicephalus: Richards, 1968: 28.
Type species: Sminthurus longisetis Guthrie, 1903.

Description

Size: females 1–2 mm, males smaller. Pigmentation very distinct, blue and red background, with yellow patches and lines (Fig. 1a, c, d). Head: eyes 8 + 8, ocelli c and d smaller (Fig. 10a). Interocular vesicles well developed; they are in fact simple eyes with the rabdome located in the posterior region of the vesicle, that receives direct light from the exterior and also possibly reflects light from the interphase tissue/ haemolymph bubble that lies below (Jordana et al., 2002). Antennal segment I with 5 setae; II with 15 setae; III with 20–24 setae, lacking papilla, and sensory organ with

sensillae in two pits (Fig. 11c); antennal segment IV without annuli and with 10 whorls of 8–10 setae (Fig. 5b), subapical cluster of 10–15 sensillae and 'peg organ' (Fig. 11a) and without apical exsertile sensory bulb. Legs: according to Richards (in Delamare Deboutteville & Massoud, 1964), oval organs and trochanteral spines absent from trochanters II and III, metatrochanters with 3 or 4 setae, depending on species; tibiotarsi: setae Ka and Kp always present, 7–11 spatulate setae (Fig. 9a–e), unguis with a single internal tooth and lateral teeth, dorsal tunica present, not visible with SEM (Figs 10c; 12c); unguiculus pointed, tapering beyond unguis, subapical filament extending beyond terminus (except for V. occidentalis, where filament is thicker than the unguiculus). Thoracic segmentation distinct (Fig. 10b). Large abdomen. Collophore with smooth sacs. Retinaculum with 2 or 3 teeth (and a basal tubercle) depending on species, always 2 + 1 in juveniles. Manubrium as long as dens and mucro together; external mucronal lamella divided by indentation, internal lamella strongly dentate, mucronal setula absent (Fig. 12d). Great abdomen includes thoracic segment II to abdominal segment IV, separation between thoracic segments II and III is distinct, more than between thoracic segment II and abdominal segment I (Fig. 10b); body setae of variable length with species-specific shapes, longest setae serrated, serrations also found on smaller setae, trichobothria in 4 pairs: a, b and c on the great abdomen, almost equidistant, forming an obtuse angle directed anteriorly, d on abdominal segment V. Abdominal segments V + VI are considered the 'small abdomen', female subanal appendage branching close to its base and directed towards genital opening, with 3 or 4 branches (Figs 1a; 6f, g; 7f), neosminthurid seta absent.

Distribution

The genus was described initially from North America, where it currently includes three species: V. longisetis, V. occidentalis and V. crossleyi. The fourth known species, V. europaeus, was found in the northern Iberian Peninsula, and a fifth, V. bellingeri, was described from the far east of Russia (Fig. 2).

Key to the Vesicephalus species

1. Lamella of unguis greatly expanded (Fig. 9b) ..... V. occidentalis
   Lamella of unguis not greatly expanded (Fig. 9c–e)..... 2
2. Dorsal setae of great abdomen pointed (Fig. 6c, d).....V. europaeus
   Dorsal setae of great abdomen truncated (Fig. 6a, b, e)…….. 3
3. Antennal segment IV = I + II …….....V. longisetis
   Antennal segment IV > I + II……...4
4. av_1' on ventral anal valve long, flattened, with some fringes (Fig. 6g)…V. crossleyi
5. av_1' short and pointed (see Bretfeld, 2002)……...V. bellingeri

VESICEPHALUS LONGISETIS (GUTHRIE, 1903)
(Figs 1a; 8a; 9a)

Sminthurus longisetis Guthrie, 1903: 51.
Neosminthurus longisetis Guthrie: Mills, 1935: 138.

S. longisetis Guthrie: Brimley, 1938: 14.
Sphyrotheca longisetis (Guthrie): Jeannenot, 1957: 411.
Sphyrotheca longisetus (Guthrie): Salmon, 1964: 594, 609.
Vesicephalus longisetis (Guthrie): Delamare Deboutteville & Massoud, 1964: 75.
Sphyrotheca longisetis (Guthrie): Dowdy, 1965.
Vesicephalus longisetis (Guthrie): Christiansen & Bellinger, 1981: 1136.
V. longisetis (Guthrie): Ardanaz & Pozo, 1985: 271.

Holotype

Labelled as 'Sminthurus longisetis Guth., Type E.25. 'Neosminthurus', bottom lands of Mississippi, Minnesota, Department of Entomology, University of Minnesota' (UMN).

Description

The original description (Guthrie, 1903) agrees with the morphological characteristics used to define the genus, but less so for the species V. longisetis. Only the holotype (Fig. 1a) was observed. It had deteriorated, having lost most of its transparency. Unfortunately, it could not be unmounted from its Canada Balsam medium. Measurements could be taken only at low magnification because of the preparation's thickness. An important detail not mentioned in the original description, confirming that it was indeed a Vesicephalus sp., was the presence of interocular vesicles. The presence of heavy, truncated macrosetae whose morphology was similar to V. occidentalis and V. crossleyi agreed with the description. The antennal segments ratio 1 : 2.4 : 2.4 : 3.4 and 1 : 2.6 : 2.8 : 3.8 for the two antennae falls well within Guthrie's formula 1 : 2.8 : 2.8 : 3.8. Antennal segment IV is not ringed, but there are clear whorls of setae. Vertex of the head, according to Guthrie (1903), with a prominent tubercle, probably by conjunction of both interocular vesicles.

The mucro agrees with the original description. Tibiotarsal chaetotaxy: first pair of legs with 6 whorls with 3, 6? 8, 8, 8 and 11 setae, respectively; a spinelike seta in whorl 2. Second pair of legs with 2, 8, 8, 8, 8 and 11 setae, with 3 thornlike setae in whorl 2, and one each in whorls 3 and 4. Third pair of legs with 4, 7, 8, 8, 8 and 11 setae, 2 thornlike setae in whorl 2 and one each in whorls 3–5 (Fig. 8a). The distal whorls of all legs with 11 setae, all clavate in the holotype (Fig. 9a). In the original description, only 4 setae are mentioned. This discrepancy was resolved using differential interference contrast (DIC) at x 100.

Biology

Guthrie describes the habitat in which he found this species as: 'deep, dark woods, under drift-wood. Quite rare'. This agrees with the habitat in which V. europaeus has been found.

VESICEPHALUS OCCIDENTALIS (MILLS, 1935)
(Figs 1b; 5d; 6a; 7a; 8b; 9b)

Neosminthurus occidentalis Mills, 1935: 138.
Eusminthurus occidentalis Mills: Salmon, 1964: 628.
Vesicephalus occidentalis Mills: Delamare Deboutteville & Massoud, 1964: 75; Christiansen & Bellinger, 1981: 1138.

Type material

Holotype: Puyallup, Washington, December, 1931; labelled as: 'Neosminthurus occidentalis Mills. Cotype, Puyallup Wash. Dec. 1931–jan 1932. W. W. Baker Det.- H. B. Mills. Illinois Nat. Hist. Survey'.

Other material

'Neosminthurus occidentalis Mills. Cotype, Olympia, Wash. XI-29-1932. H. Exline- in leaves. Det.- H. B. Mills, Illinois Nat. Hist. Survey'. 'Neosminthurus occidentalis Mills. Cotype. Puget, Wash. II-14-1932. W. W. Baker. Det.- H. B. Mills. Illinois Nat. Hist. Survey'. 'Neosminthurus occidentalis Mills. Syntype. H. B. Mills. Washington Thurston Co., Olympia, XI-29 1932. In leaves H. Exline. Mounted VI-4-81. R. J. Snider. CMCP-9' (dissection slides A1–A8). 'Vesicephalus occidentalis. Corvallis Ore. X-19-49. Leaf mould. K. Christiansen. Ill. Nat. Hist. Sur.' (seven slides with one spm. each, one slide with four spm., one slide with two spm.) (INHS).

Description

Holotype (Fig. 1b). Antenna (Fig. 5d): antennal segments ratio 1 : 3.2 : 2.4 : 3.8 (1 : 3 : 2.75 : 3.75 according to Mills); antennal segment III with a long distal macroseta, and an additional short, thick seta. Great abdomen (Figs 6a; 7a): chaetotaxy as pictured by Betsch & Bretfeld (1991). Thorax segment II with a row having 2 acuminate setae, dorsolateral macroseta and the other smaller, both with lateral serrations; beneath them, and near coxa II, a sensillum is located that is also present in the other species; thorax III with 4 macrosetae, similar to the other body macrosetae, truncate with heavy serration; row 3 (abdominal segment I), with 4 setae similar to the previous row, with the third seta placed backwards; row with a macroseta above and a mesoseta below the bothriotrichium; row with 2 setae, a dorsolateral macroseta and one acuminate mesoseta between the bothriotrichia A and B; row 6 with 2 macrosetae above bothriotrichium B, and one acuminate mesoseta and one blunt seta below; row 7 with 2 setae similar to those in row 5; the most ventral located between bothriotrichia B and C; row 8 includes bothriotrichium C, with 4 setae above and one below; ventral to the bothriotrichium C there are 2 rows of setae at right angles: series f (f1 truncate macroseta, f2/ f3 acuminate microsetae) and series i with 3 macrosetae, the last smaller and acuminate. Triangle L is recognized by setae 1, 2 and 5, lacking setae 3 and 4. Rows 9, 10 and 11 each with 2 truncated macrosetae. Tibiotarsal chaetotaxy (Fig. 8b): tibiotarsus I with 6 whorls, with 3, 7, 7, 8, 8 and 11 setae, and a spinelike seta in whorl 2; tibiotarsus II with 4, 7, 8, 7, 7 and 11 setae, with 2 thornlike setae in whorl 2 and one in whorl 3; tibiotarsus III with 4,

7(+ 1), 8, 8, 8 and 11 setae, with 2 spinelike setae in whorl 2, one in whorls 3–5 and one additional seta in whorl 2; distal whorl with 11 setae, 7 of them clavate; in the distal whorl of leg III there is some variation in the position of the clavate setae, for example between setae a, p and ai. In one of the legs III of one specimen, the short setae p and a are long and not clavate (Fig. 9b3). Unguis with tunica. Unguiculus with the subapical bristle greatly expanded at its end (Fig. 9b).

Biology

On moss (Mills, 1935).

VESICEPHALUS CROSSLEYI SNIDER, 1985

(Figs 3b; 4e; 5c; 6b, g; 7b; 8c; 9c; 10a–d)

V. crossleyi Snider, 1985: 567.

Holotype (not studied). U.S.A., Georgia, Habersham Co.

Paratypes

1♂, labelled as 'Vesicephalus crossleyi n. sp. det. R. J. Snider. Georgia, Habersham Co., Tallulah Falls, Tallulah Gorge. Leaf litter. Tullgren. March 7, 1981. R. J. Snider, colr.' (prepared for SEM); 1♂, 2 ♀♀, labelled as 'Vesicephalus crossleyi n. sp. Snider. Georgia, Habersham Co. Tallulah Falls Gorge. Leaf litter. March 7, 1981. R. J. Snider. Cmcp-9' (1♀ on eight slides; 1♀ on six slides; 1♂ on eight slides) (all in MSU).

Other material

'Vesicephalus. Female. South Carolina. Barnwell Co. Nov. 18 1983. Savannah River Plant. 83 1118-1' (1♀ on seven slides) (MSU).

Description

A paratype used for observation by SEM did not become sufficiently clean, but did allow for a clear comparison with V. europaeus. Head (Fig. 4e), chaetotaxy drawn from SEM photomicrograph; terminology adapted from Jordana et al. (1997) and Baquero et al. (2003). Antennal segments ratio 1 : 3 : 2.6 : 4.2 (1 : 2 : 4.2 : 4.2 according to Snider, 1985); 2 of the 3 macrosetae of antennal segment II are relatively short in comparison to those of V. occidentalis and V. europaeus (Fig. 5a); antennal segment III lacks macrosetae apically, 2 setae in that position are scaly (Fig. 5c). Retinaculum rami with 2 apical teeth (a neotenic character), corpus with 2 asymmetric setae. Mucro lacking setae, with a row of 5 small and subequal teeth (Fig. 10d). Great abdomen (Figs 6b; 7b): dorsal macrosetae not acuminate (Fig. 10b) and similar to those of V. occidentalis and V. bellingeri; row 1 with one sensillum and 3 very small setae (microsetae); row 2 with

4 setae (the first is a sensillum); row 3 with 5 setae (the first is a microsensillum); next there is a truncated, toothed mesoseta, and the last 3 are truncated, toothed macrosetae; row 4 contains bothriotrichium A, with 2 mesosetae below and one macroseta above; row 5 with 2 setae, a dorsal macroseta and one smooth mesoseta between bothriotrichia A and B; row 6 with 6 setae, containing bothriotrichium B (seta 5 is smooth or sensillate); row 7 with 2 setae, a macroseta and a smooth mesoseta; row 8 with 6 setae, and including bothriotrichium C, without sensilla, and with 2 setae below and three above; rows 9, 10 and 11 have 2 macrosetae each and 9 smooth setae among them. Row f with 3 setae (f1, f3/f4) and the three i setae (i1, i2 and i3). Triangle L with two setae (1 and 2). Small abdomen: the chaetotaxy of the female (Fig. 6g) as observed at SEM is different from V. europaeus and V. bellingeri: these have ventral valve setae av_1–av_5, whereas V. crossleyi seems to lack av_3; male (Fig. 3b) ventral anal valve with 5 setae, 2 of them spiniform (av_1 and av_2), possibly lacking av_3 or av_4. Leg chaetotaxy (Fig. 8c): coxa with one seta; trochanters with 4 setae, 2 ventral, one anterior and one posterior; trochanter I with one spiniform, and one reduced on trochanter III; femora with oval organs, not observable in leg II; tibiotarsus I with 3, 8, 8, 8, 8 and 11 setae, with 2 thornlike setae in whorl 2; tibiotarsus II with 4, 8, 8, 8, 8 and 11 setae, with 2 thornlike in whorl 2 and one in whorls 3 and 4, respectively; tibiotarsus III with 4, 7, 8, 8, 8 and 11 setae, between 7 and 11 clavate setae; there is great variation in the position of the clavate setae (Figs 9c; 10c).

Biology

Litter on black soil. Collected also by sweeping in ‘low mixed deciduous woods, marshy area’; Turkey oak and Sugar maple forest.

VESICEPHALUS EUROPAEUS ARDANAZ & POZO, 1985

(Figs 1c; 3a; 4a–c; 5b; 6c, d; 7c, d; 8d; 9d; 11a–k; 12a–d)

V. europaeus Ardanaz & Pozo, 1985: 271.

Holotype

♂, labelled as ‘Vesicephalus europaeus, male, Ardanaz and Pozo leg., 1985, E-1013-E, moss in oak forest of Quercus rotundifolia L. (Echauri, Navarra, SPAIN), 28-2-81’; paratypes, same data as holotype (code: E-1011-K).

Other material

SPAIN: Navarra, Sansoain, from oak forest of Q. rotundifolia (CA-0380-35), 1.xii.1982 (one specimen). – Burgos, ‘Sierra de la Tesla’, Panizares, yew forest, 15.xi.1998 (Garcia) (1♂ on slide, six spm. in alcohol, 7♂♂ and ♀♀ mounted for SEM). – ‘Sierra de la Tesla’, leaves obtained under Fagus sylvatica and Buxus sempervirens, 9.ii.2000 (one spm. in alcohol) and 2.iii.2000 (seven spm. dissected for TEM and light microscopy) (Jordana & Baquero) (all in MZNA). Also known from Vizcaya (Ardanaz & Pozo, 1985: 271).

Description

This species can be identified easily by the morphology of the dorsal, long and acuminate macrosetae (Figs 6c, d; 12b). Colour: similar to other members of the genus with the predominate yellow background with irregular polygons of violet and red over head and body (Fig. 1c, d); original description says: 'violaceous blue pigment for female and grayish blue for male, very dense over body, antennae, legs and furcula, distributed in spots that increasingly appear circular or helicoidal' (Ardanaz & Pozo, 1985). Head: typical of genus (Fig. 4a–c), clypeus with 6 setae, labrum with 5, 5, 4 setae, the latter between 3 very chitinous crests (Fig. 11e). Antenna (Fig. 5b): antennal segments ratio 1 : 2.4 : 2.4 : 3.4; joint between segments I and II as in Fig. 11(d); antennal segment II distally with 4 scaled mesosetae of same length; antennal segment III with 2 very long scaled macrosetae and one somewhat shorter; SEM made it possible to observe 12–15 blunt, smooth and cylindrical setae distally on antennal segment IV (Fig. 5b) and also a sensillum (Fig. 11b). Retinaculum with 3 apical teeth and one basal, 2 asymmetrical setae on corpus (Fig. 11k). Mucro without setae (Fig. 12d) and with a row of 6–9 subequal teeth that fuse in some specimens.

Great abdomen: all body setae are acuminate; row 1 (thorax segment II) with 3 setae, first behind sensillum of thorax segment I (Figs 6c, d; 7c, d; 11f); row 2 with 5 setae, 3 are denticulate macrosetae and 2 mesosetae; row 3 with 6 setae, with 4 and 5 set back, row 4 includes bothriotrichium A and has a seta above and 2 below; row 5 with 2 setae; row 6 includes bothriotrichium B, with 3 setae dorsal to bothriotrichium (fifth as a sensillum) and 2 ventrally; row 7 with 2 setae; row 8 with 7 setae and including bothriotrichium C (seta 3) (sixth is a sensillum, off set, absent in V. occidentalis); f series originating at bothriotrichium C has 5 setae (f2 is a sensillum); series i originates from f4, with 3 setae; triangle L with 3 setae, 1, 2 and 4; rows 9, 10, 11 with 2 macrosetae in each file, and a group of 15–17 smooth mesosetae between them; male macrosetae longer than those of female; disposition of setae are almost that of V. bellingeri, except for small setae of posterior area of great abdomen; small setae lacking M0 and DL_1 (Fig. 7f). Small abdomen: female subanal appendage typical for genus, branching near the base with 6–8 fringes; circumanal setae a_1 and a_3 very flattened from base, directed towards anal pore, similar to av_1' and av_1 branching in their distal third (Fig. 12a). Male anal valves without specialized setae, with 5 setae in series av_1, and av_1' as a microseta (Fig. 3a). Leg chaetotaxy: leg I as shown in Fig. 11(j); coxae of legs II and III with oval organs (Fig. 11g); all trochanters with 4 setae, 2 ventral, one posterior and one anterior; femora with oval organs (Fig. 11i); tibiotarsi with 6 whorls of setae on all legs; proximal whorls with 3 setae; whorls 2–5 on tibiotarsus I with 8 setae; whorl 2 with 2 thornlike setae (Fig. 11h); tibiotarsus II with 2–5 whorls of 8 setae, 2 thornlike in whorl 2 and one each in whorls 3 and 4; whorl 6 same as on tibiotarsus I; tibiotarsus III whorl 2 with 7 setae, 2 thornlike (although there are variations); distal whorl with 11 setae, 9 clavate and 2 thornlike (p and a), transpositions can happen when a´ is clavate and ja is acuminate (Figs 9d; 12c).

Biology

This species has been collected from the Iberian Peninsula in evergreen oak forests (Q. rotundifolia L.) in Echauri, Ayegui and Sánsoain (Navarra), beech forest in Vizcaya (Basque country) and mixed yew–beech forest in 'Sierra de la Tesla' (Burgos). All of

these places seem to have similar habitats, with common climatic characteristics. It appears that the species prefers low insolation, living under abrupt geological formations, and is not found in open habitats. It shares this preference with the North American species that appear to require high humidity and low light levels.

VESICEPHALUS BELLINGERI BRETFELD, 2002

(Figs 1e, f; 4d; 5a; 6e; 7e; 8e; 9e)

V. bellingeri Bretfeld, 2002: 182.

Holotype (not studied)

RUSSIA, Primorskiy Reg., NE of Vladivostok about 135ºE Gornotayozhnoye, Mountain Taiga Station; yellow pan traps, 26.-28.vi.1999 (Michailovskaya) (G. Bretfeld personal collection, Russia V/6).

Paratype

1 ♀ (no. 1, in one slide), same data as holotype.

Description

The observation of a paratype allowed us to add some complementary information to the original description. Colour: 'Background yellowish with intense brown pigment in irregular spots and marbling' (Bretfeld, 2002). Head chaetotaxy: antennae (Fig. 4d) drawn from a slide-mounted specimen. Ratio of antennal segments 1 : 2.37 : 3.2 : 4.6 (1 : 3.6 : 2.8 : 5 according to Bretfeld, 2002). Macrosetae of antennal segment II somewhat shorter than those found on V. occidentalis and V. europaeus; antennal segment III without distal macrosetae. Great abdomen: chaetotaxy of abdominal segment I (Figs 6e; 7e): dorsal macrosetae not acuminate and similar to those of V. occidentalis and V. crossleyi; row 1 with 2 macrosetae, a small seta and one sensillum in front of it; row 2 with 5 setae, last being smaller; row 3 with 7 setae, 3 macrosetae and 4 small setae; row 4 includes bothriotrichium A, with 2 mesosetae below it, and one more dorsal macroseta; row 5 with 2 setae, a macroseta and a mesoseta between bothriotrichia A and B; row 6 with 6 setae, including bothriotrichium B (seta 5 is a sensillum of the type found on V. crossleyi and V. europaeus); row 7 with 2 macrosetae; row 8 with 7 setae including bothriotrichium C (setae forward of, and immediately after, bothriotrichium C are mesosetae); rows 9, 10 and 11 with 2 macrosetae each, and 4 smooth setae between them; triangle L with 3 setae. This chaetotaxy is very similar to that observed for V. europaeus, except for the series of microsetae in the posterior setae files. Small abdomen: dorsal valve of female with av_1' short, av_1 flattened with some fringes, av_2, av_3 and av_4 long, acuminate and smooth; subanal appendage similar to other members of the genus. Leg chaetotaxy (Fig. 8e): tibiotarsus I with 3, 8, 8, 8, 8 and 11 setae, with 2 thornlike setae in whorl 2; tibiotarsus II with 4, 8, 8, 8, 8 and 11 setae, with 2 thornlike setae in whorl 2 and one in whorls 3 and 4; tibiotarsus III with 4, 7, 8, 8, 8 and

11 setae, with 2 thornlike setae in whorl 2 and one each in whorls 3–5. This distribution of the setae is exactly the same as found in V. crossleyi. Distal whorls of the tibiotarsi with 11 clavate setae (Fig. 9e).

Biology

Taken with yellow pan traps in taiga.

DISCUSSION

The genus Vesicephalus is very interesting, made so by the presence of an interocular vesicle, a curious lens-less photoreceptor with a rabdome in the upper part of the vesicle and a haemolymph bubble that reflects the light (Jordana et al., 2002). The leg chaetotaxy of V. longisetis and V. crossleyi is very similar, but there may be differences between the chaetotaxy of the first pair of tibiotarsi: it was very difficult to see the tibiotarsi of V. longisetis owing to the poor condition of the slidemounted specimen. Christiansen & Bellinger (1981) also had only one type specimen available and, on the basis of observed specimens from other localities, they stated that there may be two species involved. Likewise, they, as Guthrie (1903) and Mills (1935) previously, observed only four to five hairs on the tibiotarsus. In this study, a single specimen of V. longisetis was examined, having eleven clavate hairs. Clearly, more specimens of V. longisetis need to be collected or found in older collections to see clearly the features of this species. Another disturbing factor is the incomplete colour description for V. longisetis: to quote Mills (1935): 'brownish-black with vague yellow markings'. Other Vesicephalus species are described as having brilliant coloration with a complicated distribution of various coloured maculations. In addition, a study of the great abdomen chaetotaxy must be performed on V. longisetis to confirm its status with respect to the other members of the genus. V. europaeus is very different from V. longisetis and the other species by having acuminate setae.

V. occidentalis is separated easily by the expanded unguicular subapical filament, and with distal antennal segment III setae including a long and short heavy seta among the thornlike setae making up the whorl. V. europaeus has two very long distal setae, and both V. crossleyi and V. bellingeri have all short setae. The only character that separates V. longisetis is the ratio between the antennal segments. In V. longisetis, antennal segment IV is equal to the length of antennal segment I plus antennal segment II; the other species show antennal segment IV greater than I plus II. We can also separate V. crossleyi and V. bellingeri on the basis of the ventral anal valves of females.

The only live specimens observed are those of V. europaeus from Sierra de la Tesla (Burgos, Spain). The habitat in which they were collected was a forest of T. baccata L. (with beech, F. sylvatica L.) located in a crevasse with very high vertical walls and accumulated dead leaf litter. This habitat never receives direct sunlight. This environmental condition seems to be related to the great sensitivity of the interocular vesicles (photoreceptors), according to Jordana et al. (2002). It happens that the type locality of the species (Echauri, Navarra, Spain) also has a permanent shaded habitat in the north face of a cliff. The characteristics seem to agree between the habitat of V.

europaeus and the location in which Guthrie (1903) found V. longisetis. The genus is perhaps not holarctic but circumarctic, in effectively shaded habitats (Fig. 2). Further specimens could perhaps be collected along the northern border of holarctic continents, in front of Pleistocene glaciers (Bretfeld & Arbea, 2000; Bretfeld, 2002).

ACKNOWLEDGEMENTS

The authors wish to thank Dr Philip J. Clausen (Department of Entomology, University of Minnesota), Ms. Kathleen R. Zeiders (Illinois Natural History Survey), Mr Gary Parsons (A. J. Cook Arthropod Research Collection at Michigan State University) and Dr Gerhard Bretfeld (Zoological Institute, University of Kiel) for the loan of slides and type material for study, and Arturo Ariño for his comments.

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Figure 1. Vesicephalus spp.: a, V. longisetis, holotype in Canada balsam; b, V. occidentalis, holotype; c, V. europaeus from Burgos (Spain); d, V. europaeus, stereoscopic photograph of live specimen from Burgos (Spain); e, f, V. bellingeri, body and head of a paratype from Russia.

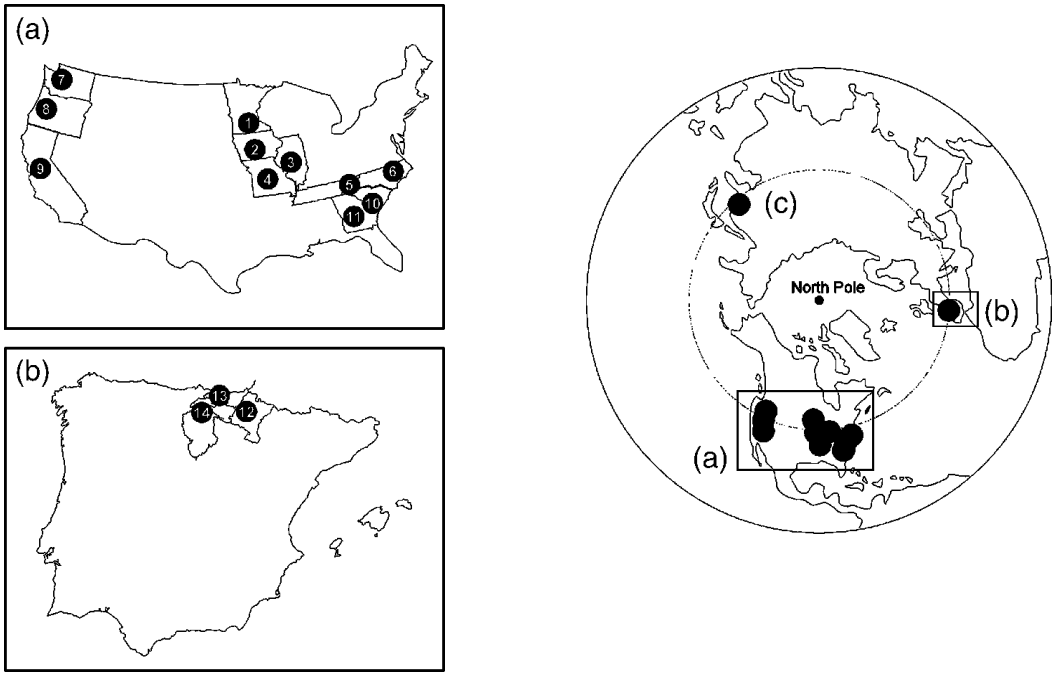

Figure 2. Distribution of the genus Vesicephalus spp. V. longisetis: 1, Bottom lands of Mississippi, Minnesota, U.S.A. (type); 2, Iowa, U.S.A. (Mills, 1935); 3, La Salle Co., Illinois, U.S.A.; 4, Missouri, U.S.A. (Dowdy, 1965); 5, Great Smoky Mountains National Park, Tennessee, U.S.A.; 6, North Carolina, U.S.A. (Brimley, 1938). V. occidentalis: 7, Puyallup, Washington, U.S.A. (type); 8, Corvallis, Oregon, U.S.A.; 9, Marin Co., California, U.S.A. V. crossleyi: 10, Habersham Co., Georgia, U.S.A. (type); 11, Savannah River Plant, Aiken Co., South Carolina, U.S.A. (Snider, 1985). V. europaeus: 12, Echauri, Navarra, Spain (type); 13, Vizcaya, Spain; 14, 'Sierra de la Tesla', Burgos, Spain (Ardanaz & Pozo, 1985). V. bellingeri: C, Mountain Taiga Station, Gonotayozhnoye, Russia (Bretfeld, 2002).

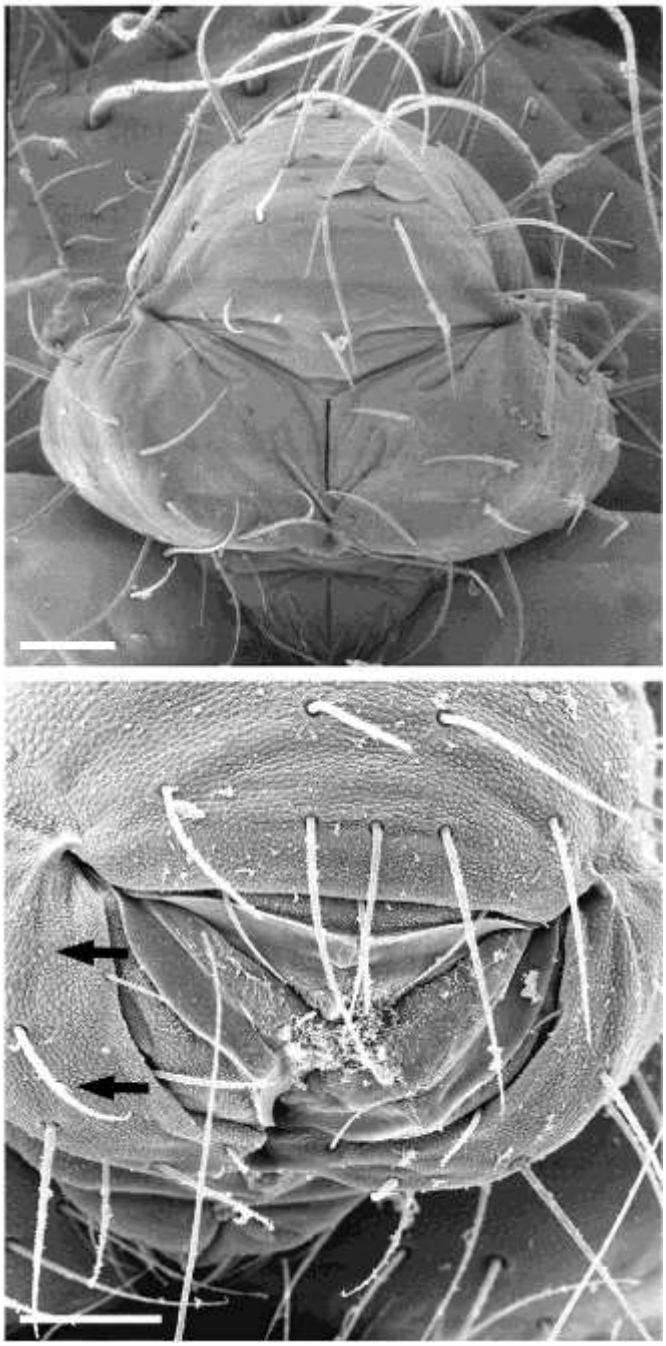

Figure 3. Vesicephalus spp. male anal valves, posterior view (scanning electron photomicrographs): a, V. europaeus (bar = 50 µm); b, V. crossleyi, arrows point to microsetae av_1' and av_2 (bar = 40 µm).

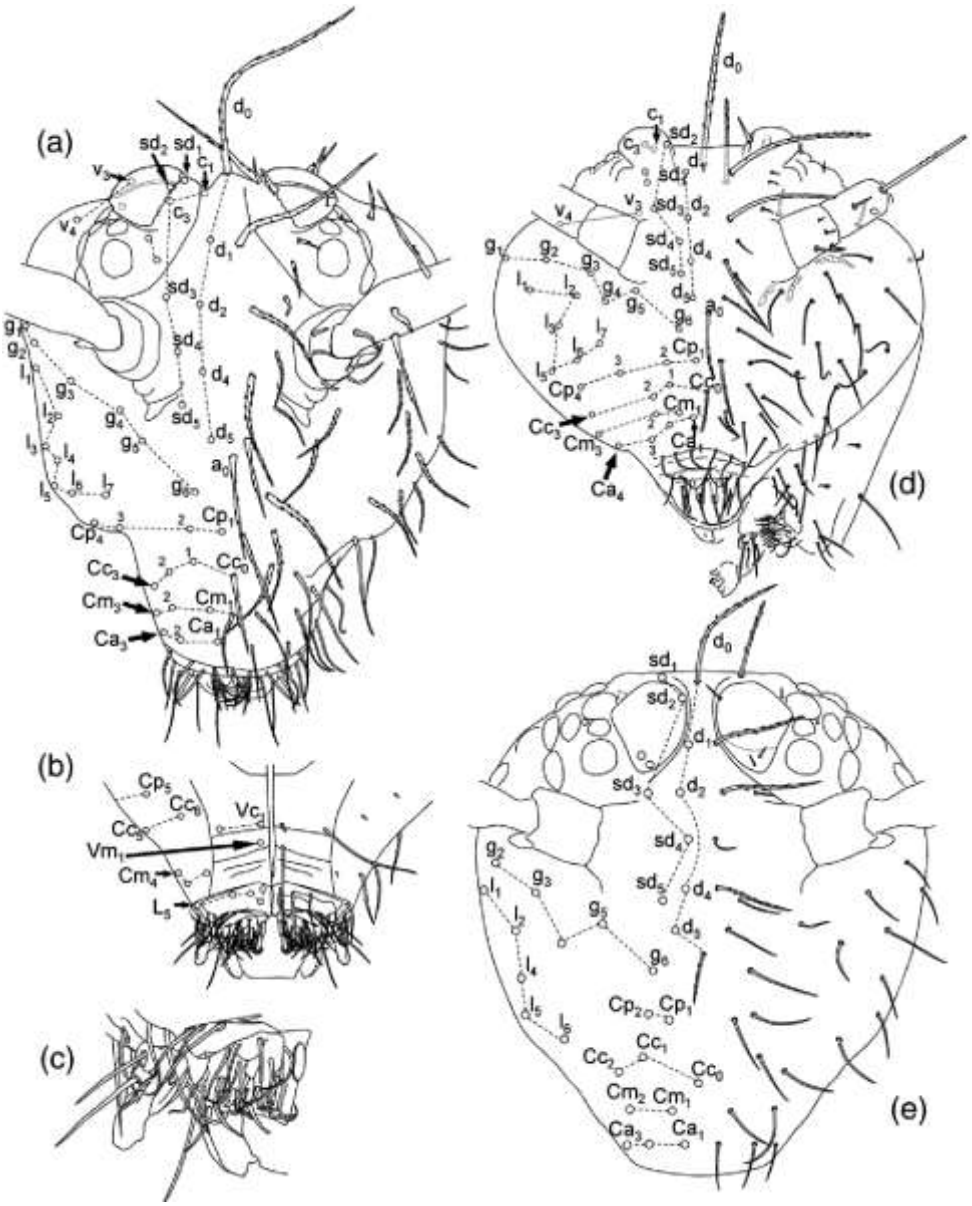

Figure 4. a, Vesicephalus europaeus, head (frontal view); **b**, V. europaeus, labium; **c**, V. europaeus, labial palps; **d**, Vesicephalus bellingeri, head (frontal view); **e**, Vesicephalus crossleyi, head (frontal view).

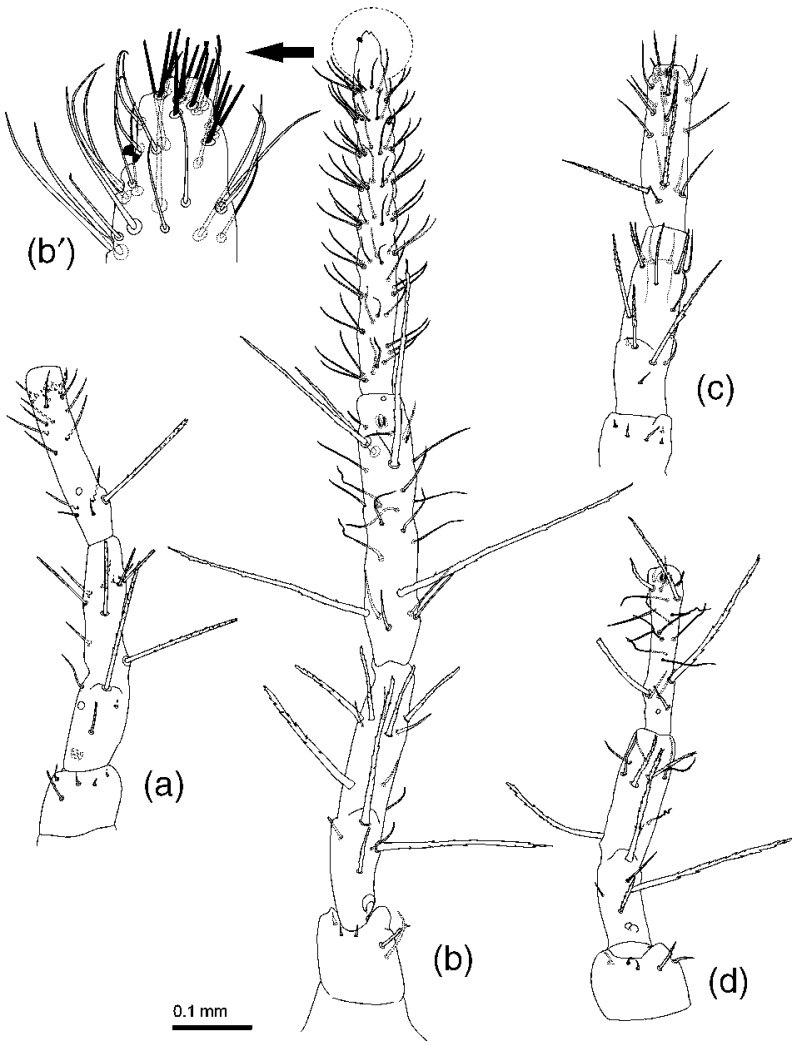

Figure 5. **a**, Vesicephalus bellingeri, antennal segments I–III; **b**, Vesicephalus europaeus, antenna (b', apical detail); **c**, Vesicephalus crossleyi, antenna; **d**, Vesicephalus occidentalis, antenna.

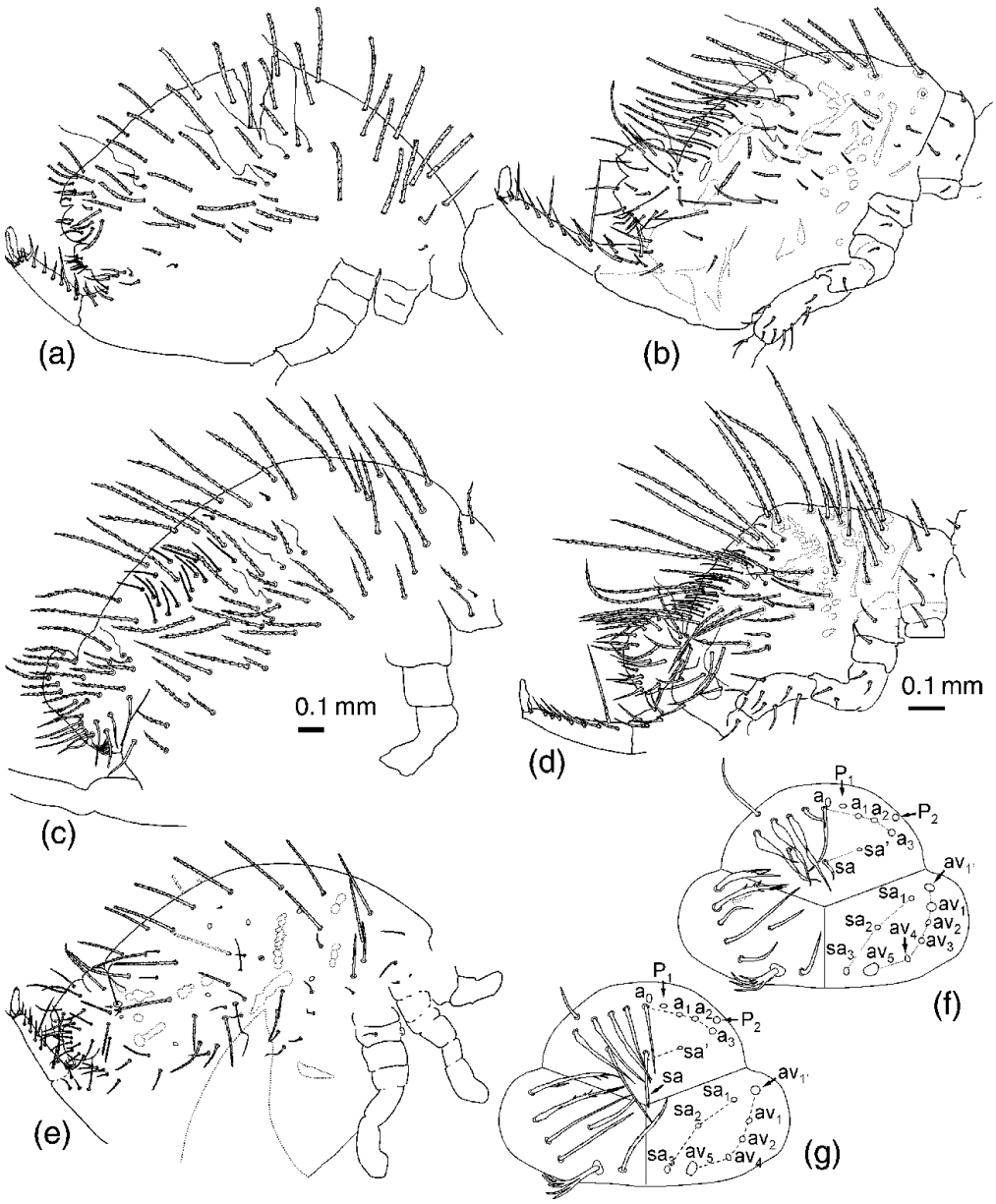

Figure 6. Vesicephalus great abdomen, lateral view and setal morphology: **a**, V. occidentalis; **b**, V. crossleyi; **c**, V. europaeus, female; **d**, V. europaeus, male; **e**, V. bellingeri; **f**, V. europaeus, female, small abdomen (posterior view); **g**, V. crossleyi, female, small abdomen (posterior view).

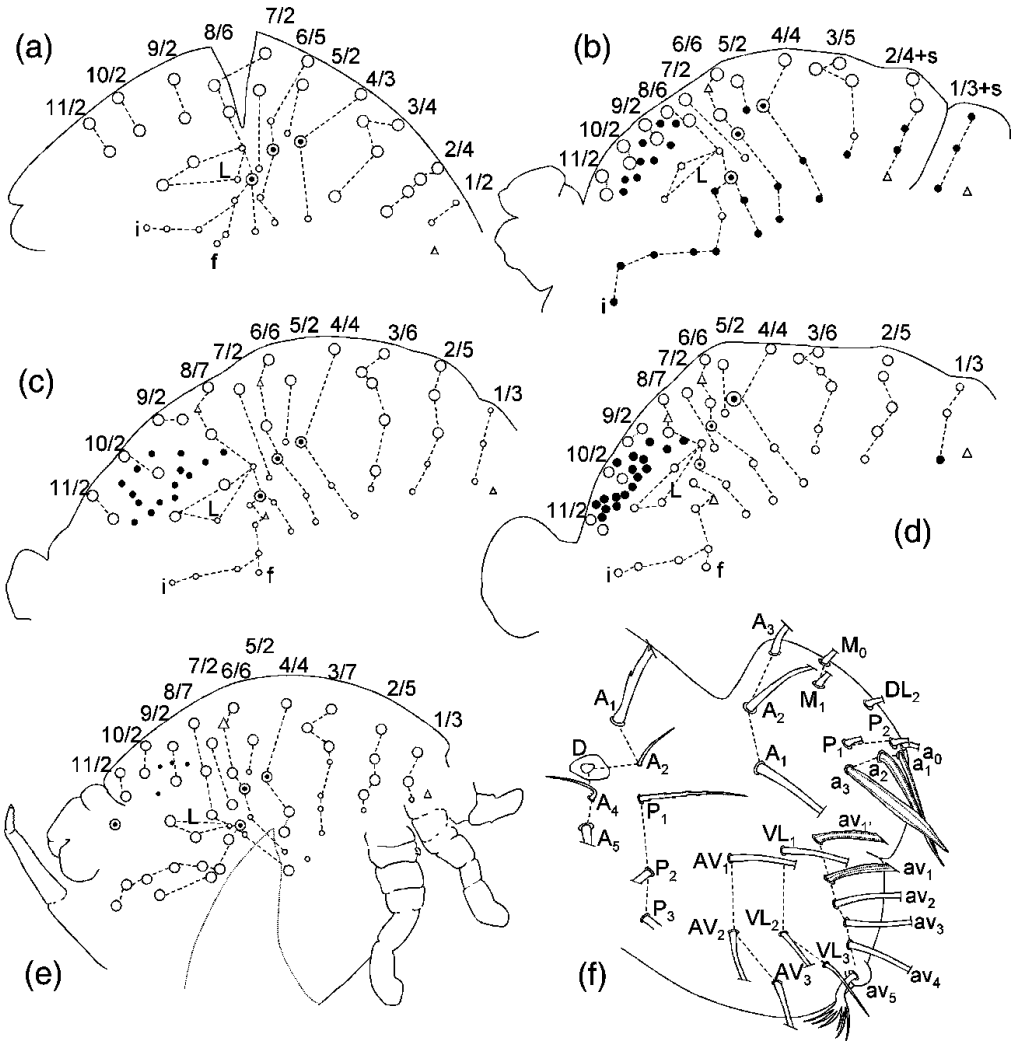

Figure 7. Vesicephalus spp., great abdomen, schematic arrangement of setae: **a**, V. occidentalis; **b**, V. crossleyi; **c**, V. europaeus, female; **d**, V. europaeus, male; **e**, V. bellingeri; **f**, V. europaeus, female, small abdomen (lateral view).

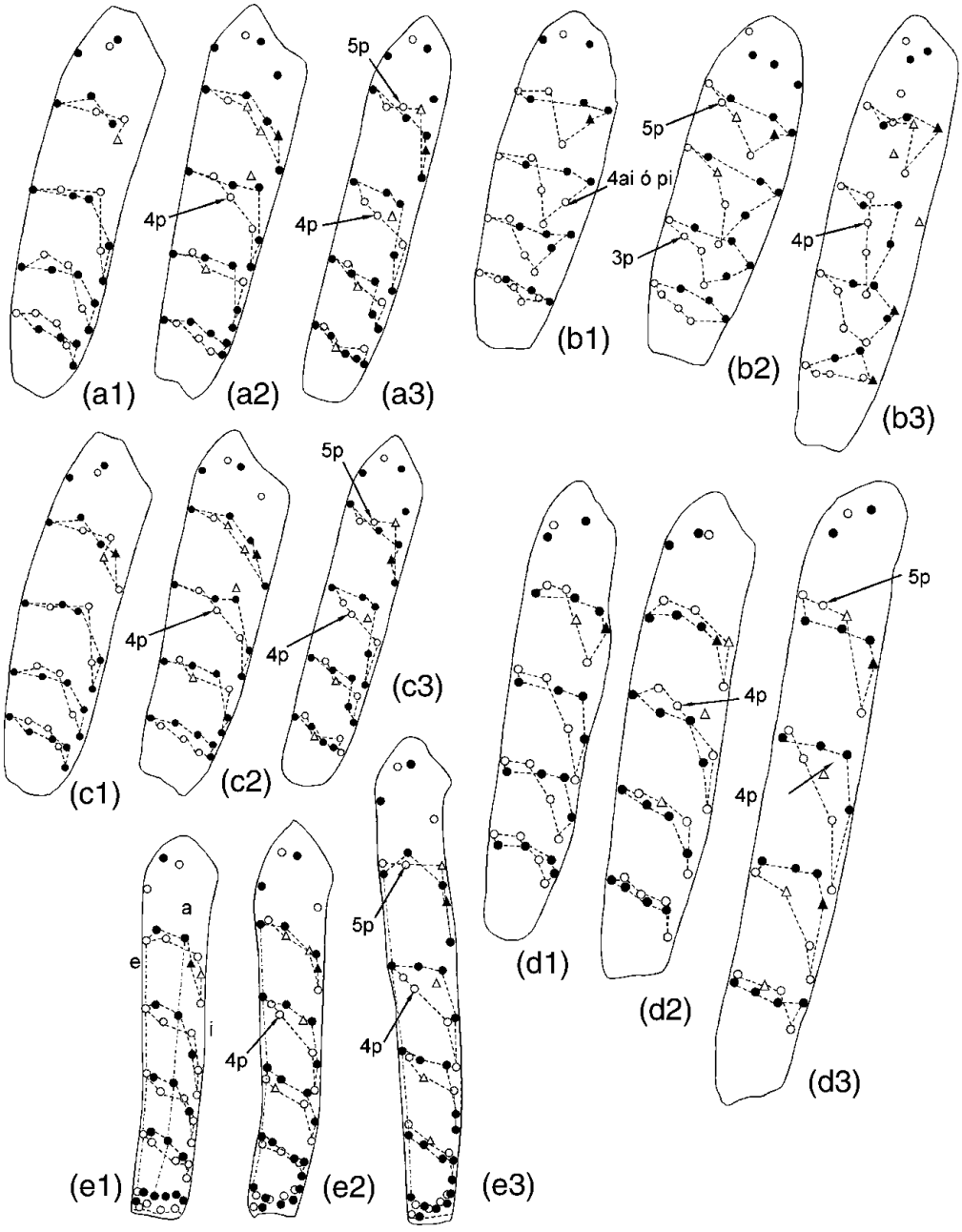

Figure 8. Vesicephalus, schematic arrangement of tibiotarsal setae: **a**, V. longisetis; **b**, V. occidentalis; **c**, V. crossleyi; **d**, V. europaeus; **e**, V. bellingeri. Symxbols: circle=seta; triangle=spinelike seta (see Fig. 11h); black=anterior; white=posterior.

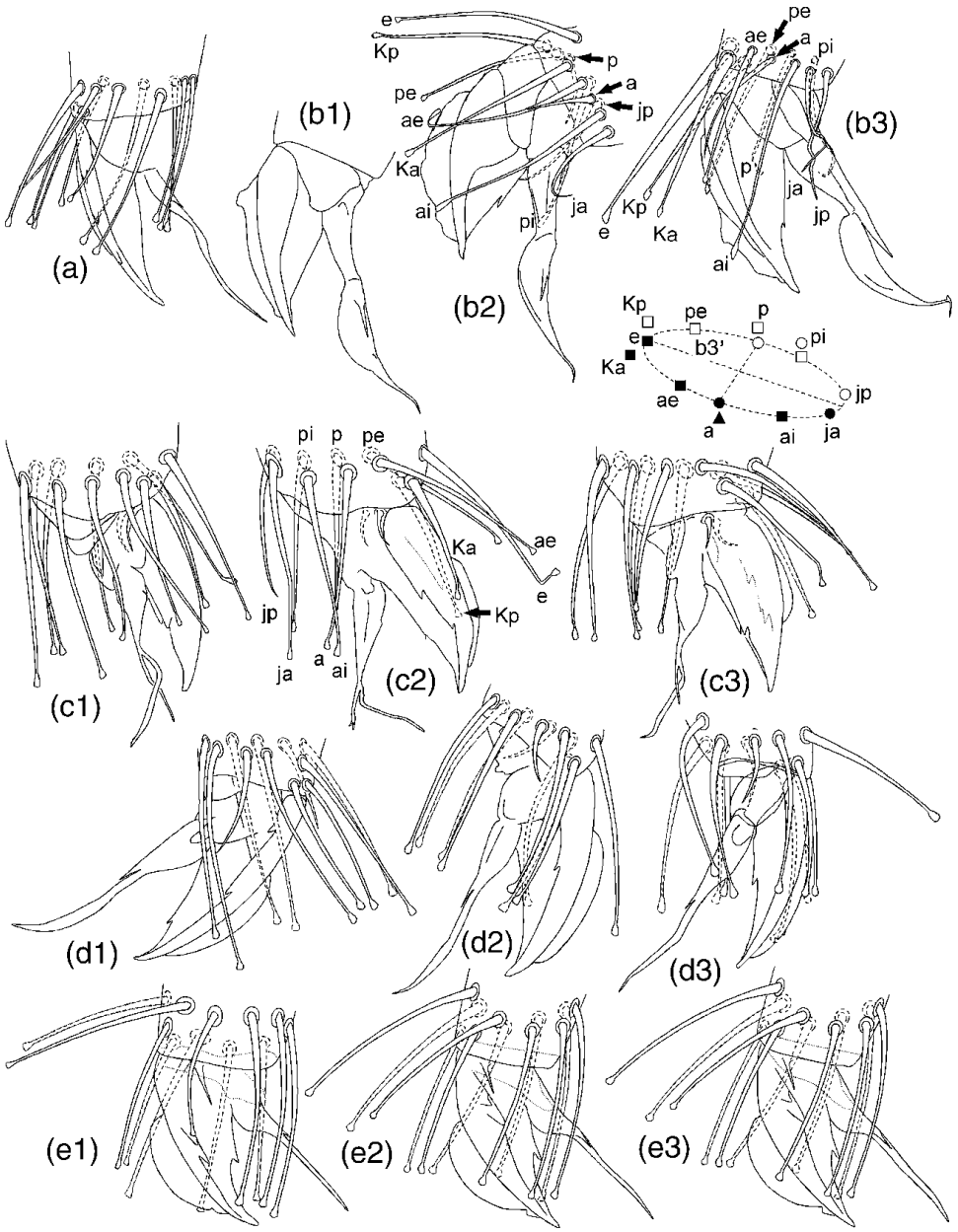

Figure 9. Vesicephalus spp., claw, unguiculus and distal tibiotarsal whorl: **a**, V. longisetis, leg 1 (legs 2 and 3 with same setae morphology); **b**, V. occidentalis [b1, leg 1; b2, leg 2; b3, leg 3; b3´, setal pattern with morphological variations (square=spatulate seta; triangle=short pointed seta; circle=long pointed seta)]; **c**, V. crossleyi; **d**, V. europaeus; **e**, V. bellingeri.

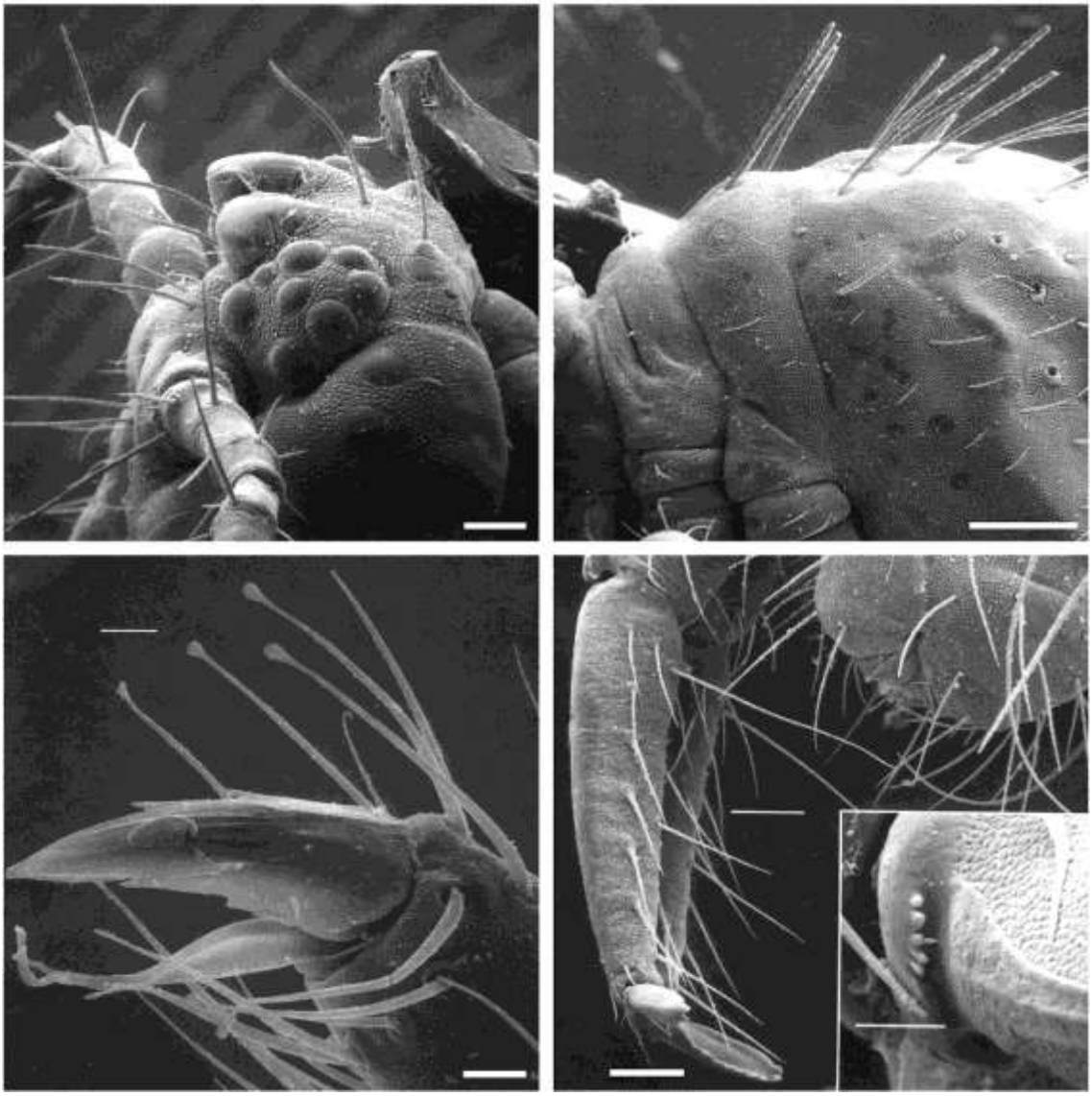

Figure 10. Vesicephalus crossleyi, scanning electron photomicrographs of a paratype: **a**, lateral view of the head (bar = 50 µm); **b**, thorax and first half of great abdomen (lateral view) (bar = 100 µm); **c**, claw, unguiculus and distal tibiotarsal whorl (bar = 10 µm); **d**, furcula (bar = 50 µm) and detail of the mucronal base.

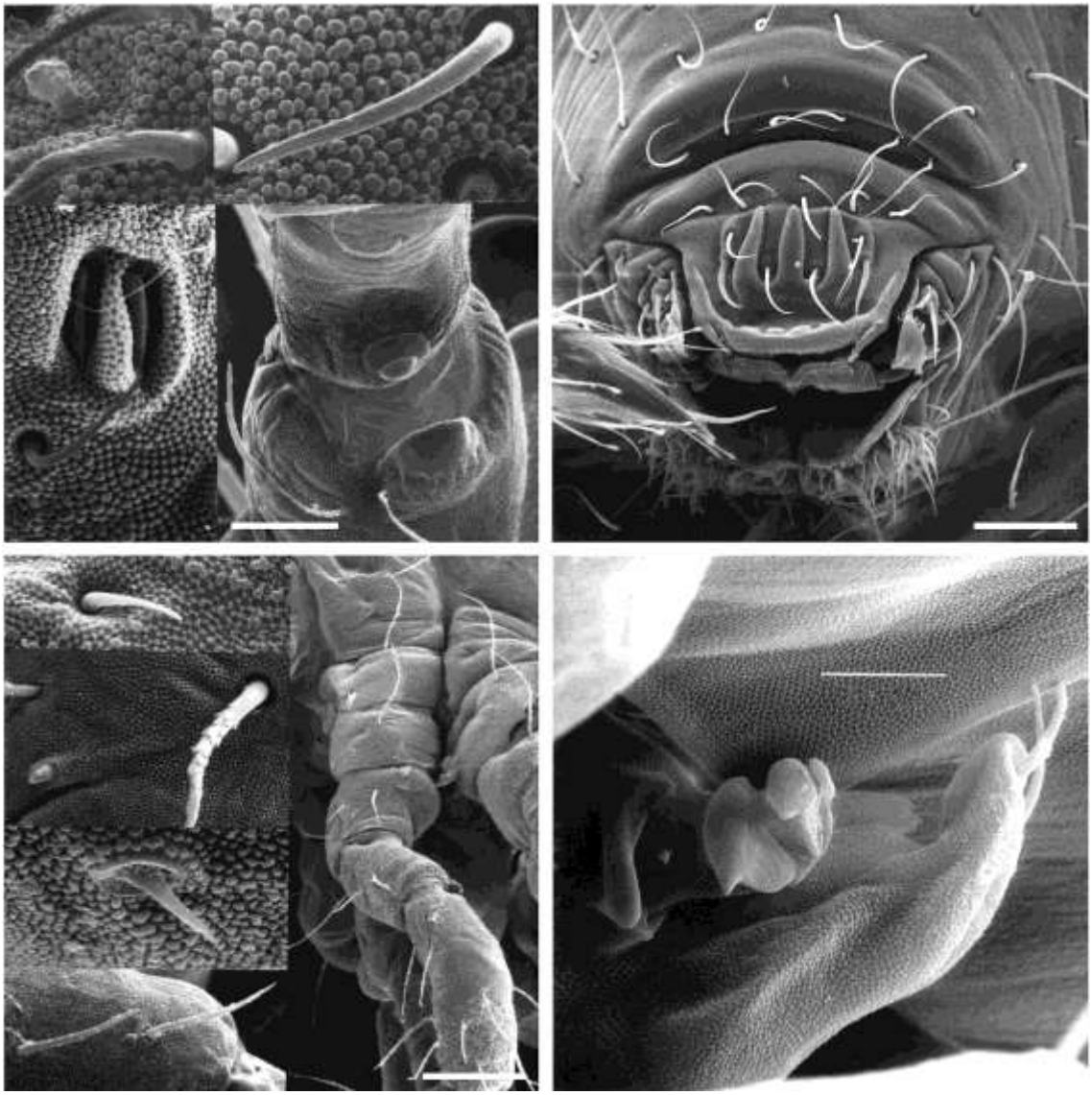

Figure 11. Vesicephalus europaeus, scanning electron photomicrographs of a specimen from Burgos (Spain): **a**, subapical microsensillum of antennal segment IV; **b**, sensillum from antenna; **c**, sensory organ from antennal segment III; **d**, joint between antennal segment I and II (bar = 10 µm); **e**, detail of clypeal and labral area (bar = 50 µm); **f**, spinelike sensillum on thorax i; **g**, trochanteral oval organ on leg I; **h**, spinelike seta on tibiotarsus I; **I**, femoral oval organ on leg I; **j**, coxae, trochanter and femur on leg I (bar = 100 µm); **k**, tenaculum and its corpus.

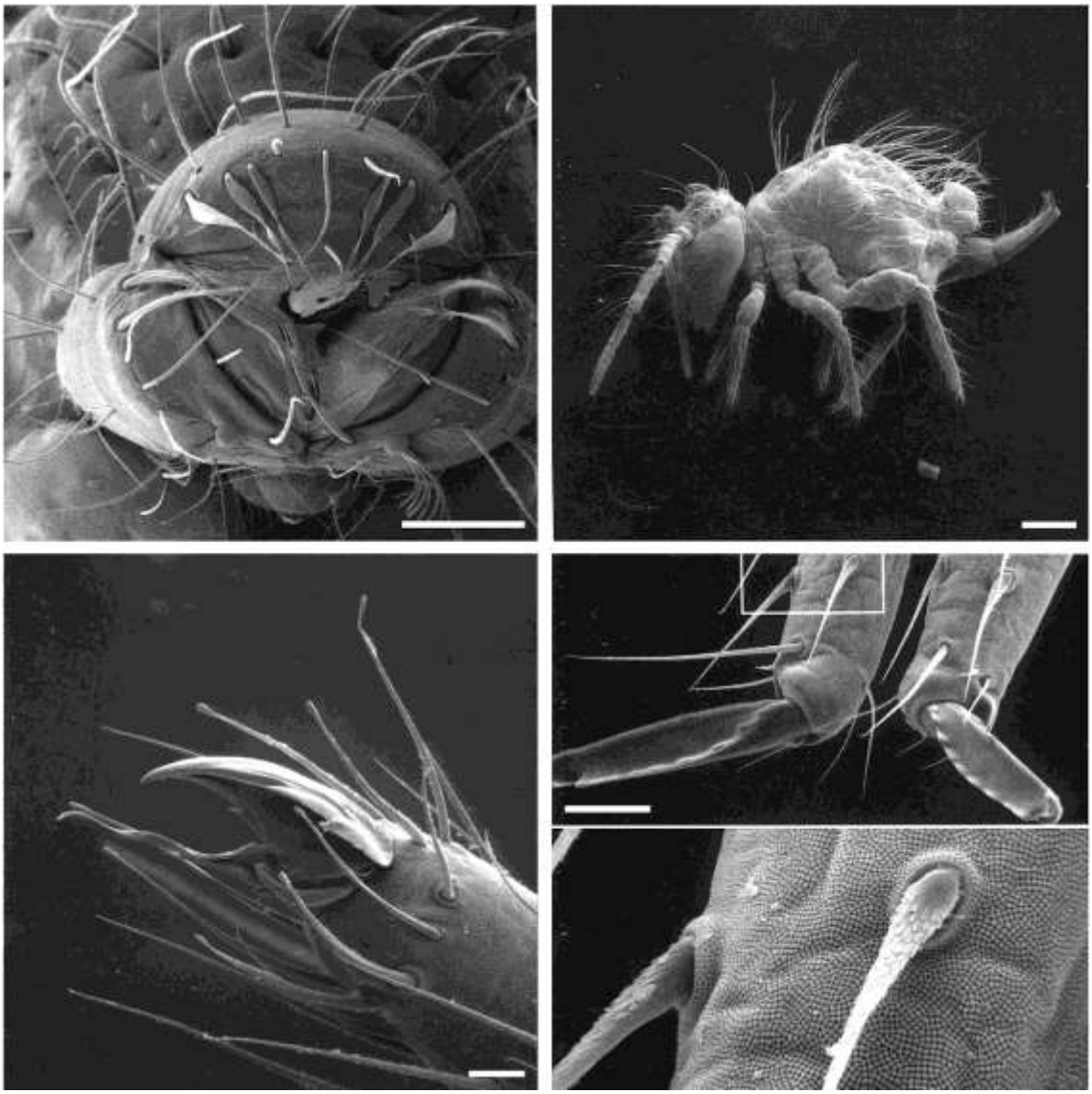

Figure 12. Vesicephalus europaeus, scanning electron photomicrographs of a specimen from Burgos (Spain): **a**, posterior view of female anal valves (bar = 100 µm); **b**, habitus of a specimen from Burgos (Spain) (bar = 200 µm); **c**, claw, unguiculus and distal tibiotarsal whorl (bar = 20 µm); **d**, distal area of furcula (bar = 50 µm) and detail of two dorsal setae (x 4).