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The genus *Acipes* Attems, 1937 in the Iberian Peninsula (Diplopoda, Julida, Blaniulidae), with the description of three new species from Spain

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Abstract. The blaniulid genus *Acipes* Attems, 1937 comprises eleven known species, distributed in Macaronesia and the Iberian Peninsula. Three of the four Iberian *Acipes* species have been recorded exclusively in subterranean environments: *Acipes andalusius* Enghoff & Mauriès, 1999, *Acipes machadoi* Enghoff & Reboleira, 2013 and *Acipes bifilum* Enghoff & Reboleira, 2013. In this work, we describe three new species of *Acipes*. Two of these species, *Acipes celtibericus* Gilgado & Enghoff sp. nov. and *Acipes oligops* Gilgado & Enghoff sp. nov., were captured in superficial subterranean habitats of central Spain. The third species, *Acipes alicantinus* Gilgado & Enghoff sp. nov., is described from specimens previously identified as *Acipes andalusius* Enghoff & Mauriès, 1999 captured in the superficial subterranean habitats in eastern Spain. We also present a comprehensive summary of the current knowledge and all available records of the Iberian *Acipes*, with a distribution map, and a key to all species of the genus. We include illustrations of the gonopods for all Iberian species. Additionally, we present the first pictures of the habitus and habitat of *Acipes andalusius* and *Acipes continentalis* Enghoff, 1986. We also provide new records of *Acipes continentalis* from subterranean and epigean habitats in several sites of Guadarrama Mountains.

Keywords. Millipedes, mesovoid shallow substratum, superficial subterranean habitats, temporal watercourses, troglobionts.

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Introduction

The majority of blaniulid species (Diplopoda, Julida) live in the soil and subterranean environments, although many species can also be frequently observed on the soil surface, under bark and in litter (Kime & Enghoff 2017). These millipedes are characterized by their slender body, relatively small size, little pigmentation, and a low number of ommatidia, or in many cases, the complete absence of eyes (Blower 1985; Enghoff *et al.* 2015). Within the Iberian Peninsula and the Balearic Islands, the family Blaniulidae comprises a total of 16 documented species, four of which belong to the genus *Acipes* Attems, 1937 (Kime & Enghoff 2017). Additionally, the genus *Acipes* includes seven Macaronesian species, distributed in Madeira (six species) and the Canary Islands (one species). Three out of the four Iberian *Acipes* species have been recorded exclusively in subterranean habitats: *Acipes bifilum* Enghoff & Reboleira, 2013, *Acipes machadoi* Enghoff & Reboleira, 2013 and *Acipes andalusius* Enghoff & Mauriès, 1999 (Enghoff & Reboleira 2013).

The study of the MSS (Milieu Souterrain Superficiel or Mesovoid Shallow Substratum), a superficial subterranean habitat constituted by a network of voids in rocky debris (Mammola *et al.* 2016), has significantly expanded our knowledge about millipede diversity and their habitat use in the Iberian Peninsula (Gilgado *et al.* 2015a, 2015b, 2015c, 2017; Akkari *et al.* 2018; Gilgado & Ortuño 2023; Gilgado 2024). However, there are few records of blaniulids in the MSS of the Iberian Peninsula. These include the species *Proteroiulus hispanus* Schubart, 1959 in Sierra Nevada, southern Spain (Gilgado *et al.* 2015b), and *Acipes andalusius* (Enghoff & Reboleira 2013; Jiménez-Valverde *et al.* 2015) in the Aitana Mountains, eastern Spain. This eastern population of the latter species is described as a new species in the present work. Additionally, Gilgado *et al.* (2017) stated that *Acipes continentalis* Enghoff, 1986 is found in syntopy with *Guadarramasoma ramosae* Gilgado, Ledesma, Enghoff & Mauries, 2017, a chordeumatidan only found in the MSS in the Guadarrama Mountains, central Spain. However, they did not specifically mention the presence of *Acipes continentalis* in the MSS. The fourth Iberian species of the genus, *Acipes continentalis*, has only been recorded in epigean environments. This species is known from eight specimens collected in three locations within the mountainous regions of central Spain (Central System), in Sierra de Gredos and Sierra de Guadarrama (Enghoff 1986; Enghoff & Mauriès 1999; Kime & Enghoff 2017).

In this study, we present: 1) new records of *Acipes continentalis* from the Guadarrama mountains, primarily collected from the MSS but also from surface habitats; 2) the description of three new species of the genus *Acipes*; 3) a comprehensive summary of the current knowledge and all available records of the Iberian species of the genus *Acipes*; and 4) a key to the species of the genus.

Material and methods

Sampling methodology

The MSS was sampled using mostly subterranean sampling devices (SSDs): a multiperforated cylinder, generally about 1 m long, buried vertically in the ground with a pitfall trap inside (Figs 1A, 2A–D). A general description of the MSS sampling methodology is provided in Gilgado *et al.* (2015c, 2017) and Gilgado & Ortuño (2023), but details varied among locations (MSS site selection, type of trap, length and number of SSDs, dates of sampling, depth of the perforated sections of the pipe, etc.) as detailed below (localities listed from North to South).

Sierra del Mencilla, in Sierra de la Demanda, Iberian System (Fig. 1A–C). We selected two sampling points, a beech forest, in Pineda de la Sierra, Burgos, coordinates 42°11′55″ N, 3°18′41″ W, with two SSDs; and a glacial circus, 42°11′21″ N, 3°18′37″ W, with three SSDs. The SSDs captured invertebrates between -50 and -90 cm. They were installed on 26 June 2017, and recovered on 18 June 2018, 22 June 2019 and 3 August 2020. Further details of the methodology are provided in Gilgado & Ortuño (2023).

Moncayo Massif, in the Iberian System (Fig. 1D). This mountain is separated by 130 km from the Sierra del Mencilla, in the same System. Two sampling points were selected, a bare scree, in Añón de Moncayo, Zaragoza, coordinates 41°46′1″ N, 1°47′01″ W, with four SSDs, and a beech forest in Tarazona, Zaragoza, coordinates 41°48′18″ N, 1°50′37″ W, also with four SSDs. The SSDs captured invertebrates between -50 and -90 cm, and they were installed on 5 June 2012, and recovered on 26 September 2012, 12 December 2012, 25 April 2013, 11 July 2013, 12 March 2014, and 2 July 2014. Further details of the sites and methodology are provided in Gilgado *et al.* (2014) and Ortuño *et al.* (2014).

Sierra del Ocejón, in Sierra de Ayllón, Central System (Fig. 2). We selected one sampling point in an alluvial MSS in a temporary watercourse (Arroyo de Valdelapuerta) in Tamajón, Guadalajara, coordinates 41°01′20″ N, 3°15′01″ W, with two 0.5 m SSDs (Fig. 1A–E) separated by 400 m. The two SSDs captured invertebrates between -25 and -50 cm. The traps were installed on 23 November 2011 and recovered monthly until 9 June 2013. Further details are explained in Gilgado & Ortuño (2015) and Ortuño *et al.* (2017). In addition, this dry watercourse was surveyed on the surface by lifting stones on 16 March 2024.

Fig. 1. Sampling technique and landscape in the Iberian System, habitat of *Acipes celtibericus* Gilgado & Enghoff sp. nov. **A**. Subterranean Sampling Device (SSD) used to sample in the MSS in Sierra de la Demanda before being covered. **B**. Glacier circus in Mencilla, Sierra de la Demanda, Burgos. **C**. Beech forest in Mencilla, Sierra de la Demanda. The pile of stones marks the position of the SSD. **D**. Scree in the Moncayo massif, Zaragoza.

Fig. 2. Sampling technique and habitat in alluvial MSS in Arroyo de Valdelapuerta, Tamajón, Guadalajara, type locality of *Acipes oligops* Gilgado & Enghoff sp. nov. **A**. Removal of Subterranean Sampling Device (SSD) lid. **B**. Retrieval of pitfall trap from the SSD. **C–D**. Removal of the SSD tube (0.5 m) at the end of sampling period. **E**. Structure of the debris and voids in the alluvial MSS as seen after removal of the tube (microhabitat of *Acipes oligops* sp. nov.). **F**. Temporal watercourse (Arroyo de Valdelapuerta) and surrounding vegetation (habitat of *Acipes oligops*).

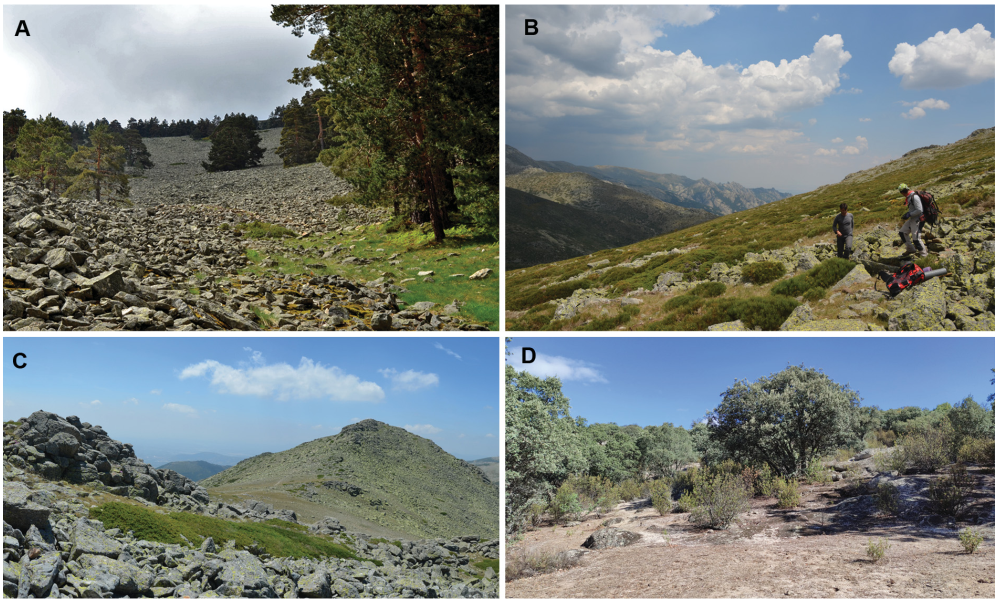

Fig. 3. Habitat of *Acipes continentalis* Enghoff, 1986. **A**. Falda del Cerro de la Muela, Sierra de Guadarrama, Segovia, 1605 m. **B**. Landscape in the highest sampling point, scree between Cabeza de Hierro Mayor and Menor (peak at the right), Sierra de Guadarrama, Madrid. **C**. Landscape of La Maliciosa, Sierra de Guadarrama, Madrid. **D**. Landscape in La Cabrera, Sierra de Guadarrama, Madrid.

Sierra de Guadarrama, in the Central System (Fig. 3). We selected 33 sampling points, placing one SSD per site, except two sites where a shorter tube (0.5 m) was installed beside the regular one. The SSDs captured invertebrates between -50 and -90 cm, except for the two shorter SSDs, which captured between -20 and -50 cm. In addition, two sampling points were surveyed by two buried pitfall traps each, following the methodology explained in Giachino & Vailati (2010). All sampling sites were distributed along the inverted T-shaped mountain range, spanning over 65 km. The SSDs were installed at different dates, from 20 May 2015 to 9 July 2015, and collected after a period of four months (17 September 2015 to 6 November 2015), a second period of eight months (24 May 2016 to 13 July 2016) and a third period of three months (up to 14 October 2016). Further details of the methodology and sampled localities in this mountain range are provided in Baquero *et al.* (2017), Gilgado *et al.* (2017) and Ortuño *et al.* (2022). Given the high number of sampling points and dates, we are only providing the coordinates of the sampling points and dates of capture for each capture in the examined material sections below.

Sierra de Mariola, in the Baetic System (Fig. 4A). We selected two screes, 2.2 km apart: one in Agres, Alicante, coordinates 38°46′21″ N, 0°29′55″ W, and one in Cocentaina, Alicante, coordinates 38°45′22″ N, 0°28′57″ W (Fig. 4B), with four SSDs each. The SSDs captured invertebrates between -20 and -90 cm. The SSDs were installed on 8 October 2011 and recovered 16 January 2012, 19 April 2012, 11 July 2012, 24 October 2012, 9 May 2013 and 14 January 2014. Beside each SSD a surface pitfall trap was installed. Further details of the sites and methodology are provided in Gilgado *et al.* (2015c).

Sierra de Aitana, in the Baetic System (Fig. 4B). One sampling point in a bare scree in Confrides, Alicante, with eight SSDs, 38°39′26″ N, 0°17′54″ W. The SSDs captured invertebrates between -20 and -90 cm. They were installed on 25 July 2011 and recovered on 28 October 2011, 26 January 2012, 29 April 2012, 27 July 2012, 1 November 2012, 16 May 2013, 20 November 2013. Details of the site and methodology are provided in Gilgado *et al.* (2015c) and Jiménez Valverde *et al.* (2015). Beside each SSD a surface pitfall trap was installed.

Additional records. Actively captured specimens were hand-collected in caves (Fig. 5) and on the surface and then introduced in vials with 70% ethanol.

Specimen study and repositories

The specimens were examined using a Nikon SMZ800 or a Wild M10 stereo microscope and a Leica DM 2500 microscope. Photographs were taken with a Nikon D5100 camera mounted on the first

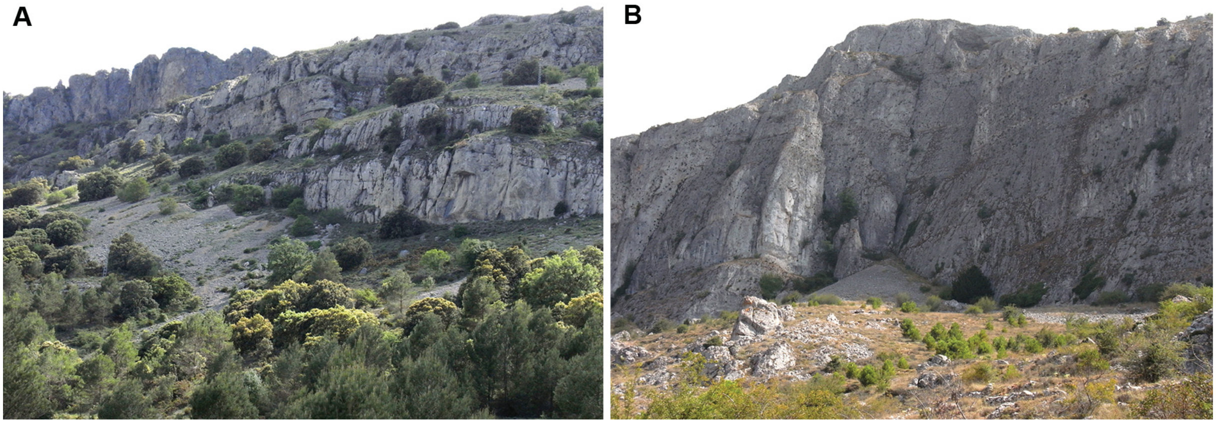

Fig. 4. Habitat of *Acipes alicantinus* sp. nov. Gilgado & Enghoff. **A.** Scree in Sierra de Mariola, Alicante. **B**. Scree in Sierra de Aitana, Alicante.

two microscopes. Gonopods and legs of *Acipes oligops* sp. nov. were placed in temporary glycerine mounts and photographed with an Olympus BX51 microscope with Nomarski differential interference contrast. Specimens for Scanning Electron Microscopy (SEM) were dehydrated in several baths of absolute ethanol and acetone. They were coated with gold (University of Alcalá) or platinum (only *Acipes oligops* sp. nov. in the Natural History Museum of Vienna). SEM photographs were taken in the microscopy service of the University of Alcalá, with a JEOL JSM-IT500, or in the Natural History Museum of Vienna, with a JEOL JSM-6610LV.

Studied material is stored in the University of Alcalá (UAH), Madrid, Spain; the Natural History Museum of Denmark (NHMD), Copenhagen; and in the Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain.

Fig. 5. Habitat of *Acipes andalusius* Enghoff & Mauriès, 1999. Cave PB-4, Peal de Becerro, Jaén. Photograph by Toni Pérez (GEV).

Image preparation

The habitus and gonopods photographs were stacked with Helicon Focus. The drawings and all figure plates were elaborated with Photoshop CS 8.0.1 and Photopea (https://www.photopea.com). The distribution map (Fig. 6) was made with QGIS 2.18 and Photoshop CS 8.0.1.

Abbreviations

af = apical flange of posterior gonopods
apo = tibial apophysis of first male legs
cxp = coxal process of anterior gonopods
ft = filamentous tip of posterior gonopods
ta = tarsus remnant of first male legs
tp = telopodite of anterior gonopods

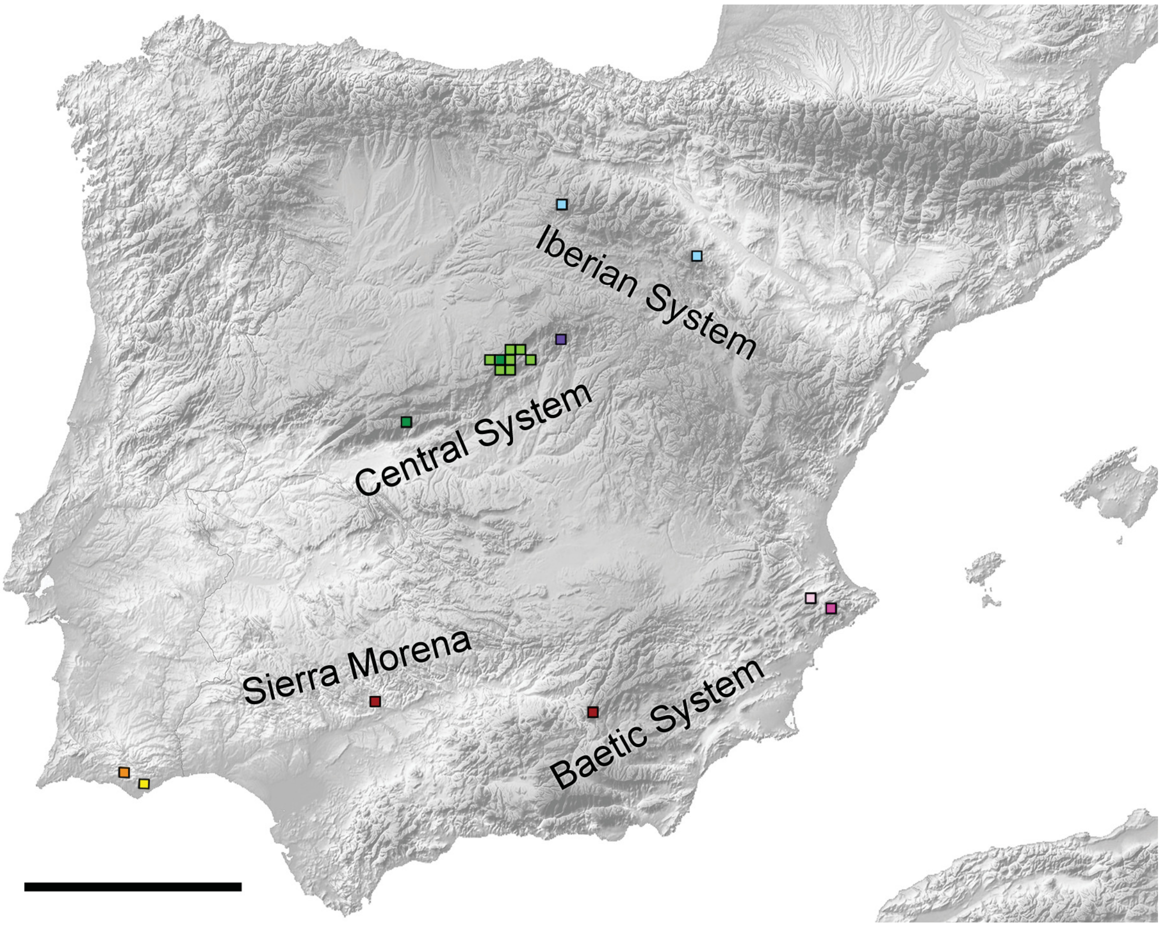

Fig. 6. Distribution of the species of *Acipes* in 10 × 10 km UTM squares in the Iberian Peninsula. Main mountain systems with *Acipes* Attems, 1937 records are labelled. Blue squares: *Acipes celtibericus* Gilgado & Enghoff sp. nov. Purple square: *Acipes oligops* sp. nov. Gilgado & Enghoff. Dark green squares: previous records of *Acipes continentalis* Enghoff, 1986. Light green squares: new records of *Acipes continentalis*. Dark red squares: *Acipes andalusius* Enghoff & Mauriès, 1999. Light pink square: new record of *Acipes alicantinus* sp. nov Gilgado & Enghoff. Dark pink square: previous record of *Acipes alicantinus* sp. nov.(as *A. andalusius* in the literature). Orange square: *Acipes machadoi* Enghoff & Reboleira, 2013. Yellow square: *Acipes bifilum* Enghoff & Reboleira, 2013. Scale bar = 200 km.

Results

In the present work we have analysed 841 individuals of *Acipes*, collected mostly in the MSS, of which 39 belong to *Acipes alicantinus* sp. nov. (Figs 7C, 8–9), three belong to *Acipes andalusius* (Figs 7A–B, 10), 700 to *Acipes celtibericus* sp. nov. (Figs 7D, 12–15), 97 to *Acipes continentalis* (Figs 7E, 16), and two to *Acipes oligops* sp. nov. (Figs 7F, 17).

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844
Order Julida Brandt, 1833
Family Blaniulidae C.L. Koch, 1847

Genus ***Acipes*** Attems, 1937

Type species

Acipes atlanticus Attems, 1937.

Diagnosis (modified from Enghoff 1983)

When present, ommatidia in a more or less regular row. First pair of male legs incrassate (except in *A. machadoi*) with one or two tibial apophyses (except in *A. machadoi*). Anterior gonopods with separate, apically dilated coxal apophyses, telopodites without setae. Posterior gonopods with a slender, curved shaft carrying a ventral rugose furrow, apically with a dorsal or lateral flange (no flange in *A. waldeni* Enghoff, 1983 and *A. bifilum*). Vulvae without setae. Operculum much longer than bursa, rugose, apically emarginate. Bursa subspherical, with a subspherical to subcylindrical receptaculum seminis.

Acipes alicantinus Gilgado & Enghoff sp. nov.

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Figs 7C, 8–9

Acipes andalusius – Enghoff & Reboleira 2013: 488. — Jiménez-Valverde *et al.* 2015: table S1.

Diagnosis

Acipes alicantinus sp. nov. differs from the other *Acipes* species by the following combination of characters: absence of eyes (eyes present in *A. atlanticus*, *A. celtibericus* sp. nov., *A. continentalis*, *A. decolor* Enghoff, 1983, *A. franzi* (Loksa, 1967), *A. lateralis* Enghoff, 1983, *A. oligops* sp. nov., *A. portosantoensis* Enghoff, 1983, *A. serratus* Enghoff, 1983 and *A. waldeni*); flange in posterior gonopods present (absent in *A. bifilum*); first pair of legs of male modified, with no claw visible (not modified and with visible claw in *A. machadoi*); tibiae of first pair of legs of male slender, more than twice as long as wide, subapical emargination of coxal process of anterior gonopods subtle and distalmost part of anterior gonopods, narrower than prior to the emargination, flange of posterior gonopods lanceolate, accessory claw in midbody legs not visible (tibiae of first pair of male legs around 1.5 times as long as wide, coxal process of anterior gonopods similar in width along all their length, flange of posterior gonopods truncate or rounded, accessory claw of midbody legs visible in *A. andalusius*).

Etymology

The specific epithet '*alicantinus*', refers to the province of Alicante, where this species was found, adjective.

Type material

Holotype

SPAIN • ♂; Alicante, Confrides, Sierra de Aitana, MSS; 38°39′26″ N, 0°17′54″ W; 1350 m a.s.l.; 16 May 2013 (trap set on 1 Nov. 2012); J.D. Gilgado, V.M. Ortuño *et al.* leg.; MNCN 20.07/2169.

Paratypes

SPAIN • 5 ♂♂, 2 ♀♀; same collection data as for holotype; MNCN 20.07/2170-76 • 2 ♂♂, 1 ♀; same data as for preceding; 24 Mar. 2012 (trap set on 26 Jan. 2012); NHMD.

Other material examined

SPAIN • 8 ♂♂, 1 ♀; same data as for holotype; 27 Jul. 2012 (trap set on 24 Apr. 2012); NHMD • 2 ♂♂, 6 juveniles; same data as for holotype; 16 May 2013 (trap set on 1 Nov. 2012); UAH • 5 ♂♂; same data as for holotype; 30 Nov. 2013 (trap set on 16 May 2013); UAH • 1 ♂; Cocentaina, Sierra de Mariola, Montcabrer, near Mas de Llopis, MSS; 38°45′22″ N, 0°28′57″ W; 1210 m a.s.l.; 19 Mar. 2012 (trap set on 13 Jan. 2012); J.D. Gilgado, V.M. Ortuño *et al.* leg.; NHMD • 2 ♂♂, 3 ♀♀; same data as for preceding; 14 Jan. 2014 (trap set on 9 May 2013); UAH.

Description

Light brown to pale amber colour in preserved specimens (Fig. 7C). Males 7–11 mm long, and 0.68 mm in maximum vertical diameter, with 29–40 podous rings including collum + 2–4 apodous rings + telson. Measures taken on five randomly chosen males. Females 11–13 mm long, and 0.7 mm in maximum height, with 38–43 podous rings including collum + 2 apodous rings + telson. Measures taken on five randomly chosen females.

HEAD. Males with parrot beak modification of cardo and stipes (Fig. 8A–B). Labrum with 3 teeth and 6+6 labral and 2+2 supralabral setae (Fig. 8B). Cephalic capsule with a few smaller setae laterally, 1+1 short setae on frons, and 1+1 long setae on vertex. Eyeless. Antenna with antennomere 5 with a distal ring of thick sensilla basiconica, antennomere 6 with half such ring of thinner sensilla (sensilla absent ventrally), and antennomere 7 with a dorsodistal row of smaller sensilla basiconica (Fig. 8A, C). Antennomere lengths (mm): 0.05, 0.22, 0.22, 0.19, 0.21, 0.16, 0.06, 0.04.

TRUNK. Collum with 4+4 setae. Rings of anterior part of body with 5+5 metazonital setae, increasing to ca 14 at midbody rings, and 16+16 at final body rings (Fig. 8D–E). Length of midbody setae around 22% of midbody ring height. 6 to 7 striae in ventral half of the ring. Telson: epiproct with 1+1 long dorsal, 3+3 lateral, and 1+1 ventral setae (Fig. 8E). Hypoproct with 1+1 setae, and paraprocts with 2 setae each.

LEGS. First pair of male legs modified, with no visible claw (Fig. 8F). Tibiae of first pair of legs of male slender, more than twice as long as wide, and with two stout apophyses, and tarsus remnant reduced, almost absent. Legs of first half of body of males with up to six lanceolate, transversely striate setae on femur (1–2), postfemur (2) and tibia (2) (Fig. 8G). Number of lanceolate setae decreasing towards and after midbody legs, absent in posteriormost third of the body (Fig. 8H). Lanceolate setae absent in females. Accessory claw in midbody legs not visible, but present in anteriormost legs (Fig. 8G–H).

ANTERIOR GONOPODS. Coxal process (*cxp*) with subapical emargination subtle, almost absent, distalmost part narrower than prior to the emargination. Telopodites (*tp*) around a third of the length of coxal processes (Fig. 9A, C).

POSTERIOR GONOPODS. Curved, distal part anteriorly serrulate, including a filamentous tip (*ft*), and distal lanceolate flange (*af*) with apical margin serrulate (Fig. 9B, D).

Fig. 7. Habitus of *Acipes* Attems, 1937 species studied in the present work. **A**. Living specimen of *Acipes andalusius* Enghoff & Mauriès, 1999 from cave PB-4. Photograph by Toni Pérez (GEV). **B**. Dissected male specimen of *Acipes andalusius* from PB-4 cave; UAH. **C**. Male specimen of *Acipes alicantinus* Gilgado & Enghoff sp. nov. from Aitana mountain; MNCN 20.07/2169. **D**. Male specimen of *Acipes celtibericus* Gilgado & Enghoff sp. nov. from Mencilla, Sierra de la Demanda, Burgos; MNCN 20.07/2106. **E**. Male specimen of *Acipes continentalis* Enghoff, 1986 from Rascafría, Sierra de Guadarrama, Madrid. UAH. **F**. Male paratype of *Acipes oligops* sp. nov. Gilgado & Enghoff, MNCN 20.07/2167. Scale bar = 2 mm.

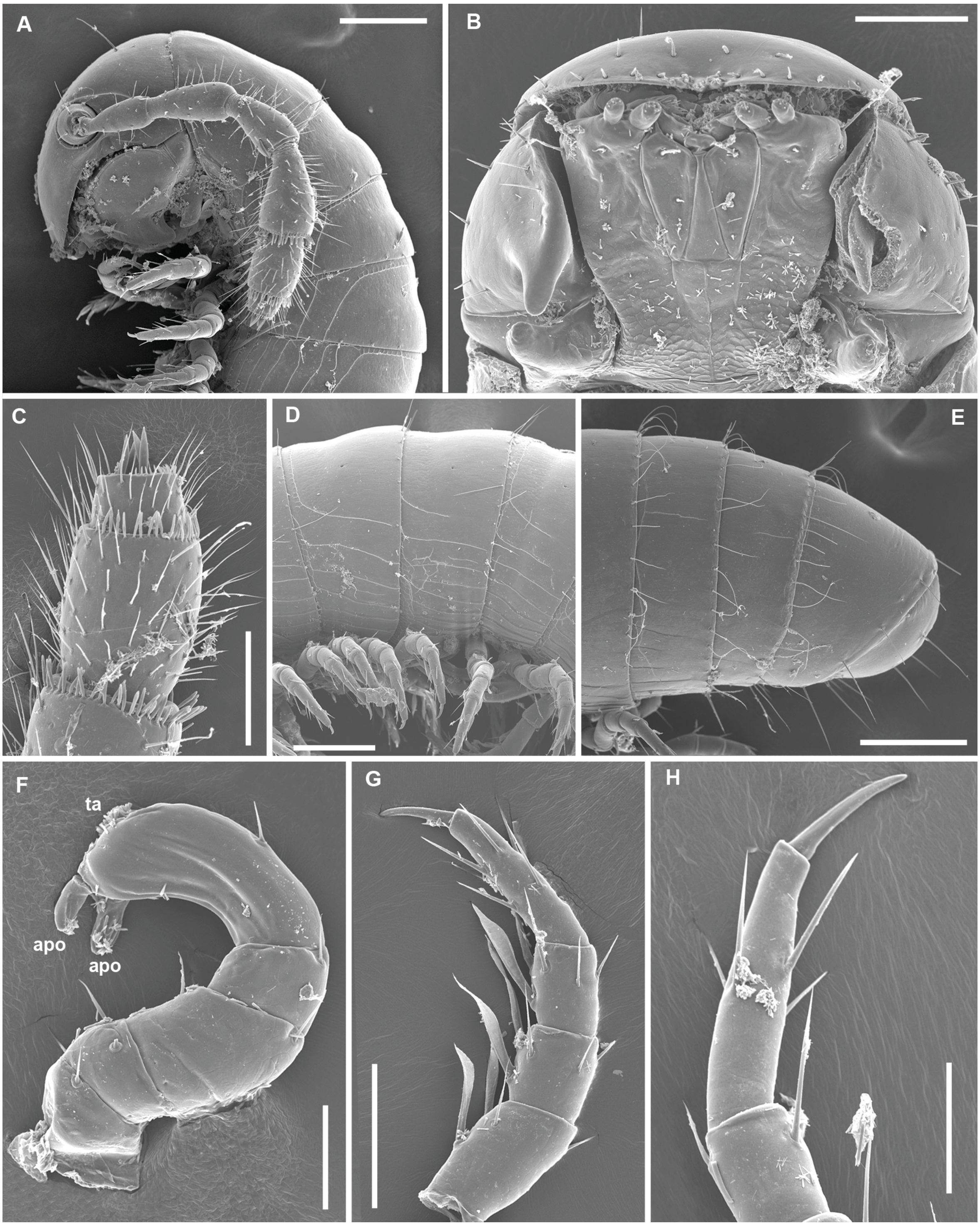

Fig. 8. Anatomical details of *Acipes alicantinus* sp. nov. Gilgado & Enghoff. **A.** Head and first five rings of male specimen from type locality in left lateral view; 30 Nov. 2013; UAH. **B**. Head of another male specimen from same locality and date in ventral view; UAH. **C**. Tip of antenna of same specimen as A in dorsal view. **D**. Rings 6–9 of same specimen as A. **E**. Telson and last body rings of same specimen in left lateral view. **F**. First male legs of same specimen as B in posterior view. **G**. Leg 4 of same specimen as B. **H**. last leg of same specimen as B. Abbreviations: *apo* = tibial apophysis; *ta* = tarsus remnant. Scale bars: A, D–E = 0.2 mm; B–C, G = 0.1 mm; F–H = 0.05 mm.

Type locality

The type locality is a colluvial debris slope at the base of Peña Cacha in the Sierra de Aitana massif, Alicante (Fig. 4A). This mountain range has the highest peak in Alicante (1558 m a.s.l.). The bedrock consists of Eocene limestones (Alfaro *et al*. 2006), whose fragmentation during the cold Quaternary periods formed the debris (Marco 2000). The climate features extremes, with summer temperatures

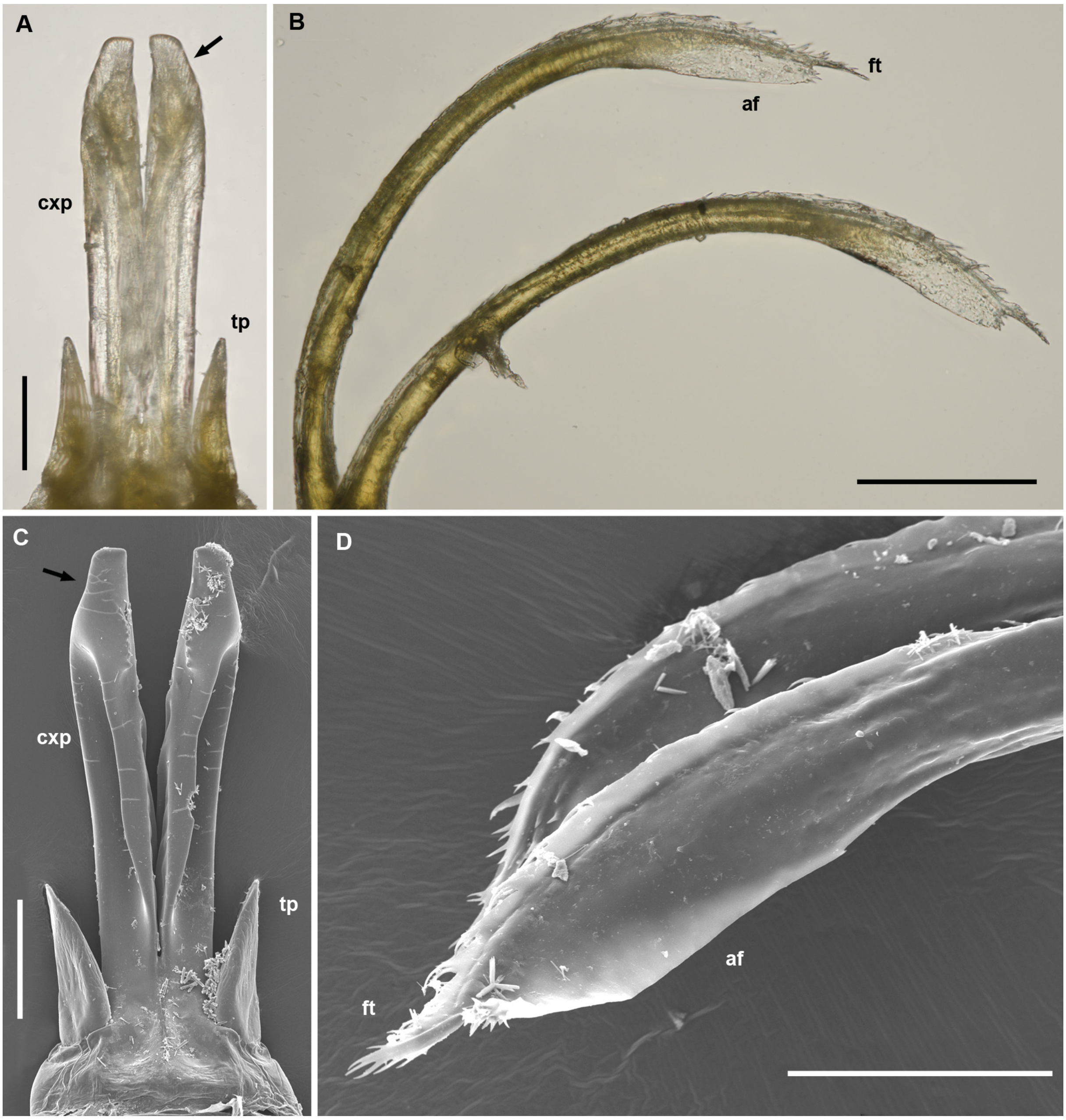

Fig. 9. Gonopods of *Acipes alicantinus* Gilgado & Enghoff sp. nov. **A**. Anterior gonopods of holotype in posterior view. MNCN 20.07/2169. Arrow indicates subapical emargination of coxal process. **B**. Posterior gonopods of holotype in right lateral view. MNCN 20.07/2169. **C**. Anterior gonopods of male specimen from type locality (30 Nov. 2013) in posterior view. Arrow indicates subapical emargination of coxal process. **D**. Detail of flange and filamentous tip of posterior gonopods of same specimen as C in left lateral view. Abbreviations: *af* = apical flange; *cxp* = coxal process; *ft* = filamentous tip; *tp* = telopodite. Scale bars: A–C = 0.1 mm; D = 0.05 mm.

exceeding 30 °C and winter snow cover. Annual precipitation ranges between 800 and 900 mm. The debris forms scree and colluvial fans, partially covered by sparse soil and vegetation. Sierra de Aitana represents a high Mediterranean mountain environment of significant biogeographic interest (Marco 2001). It harbours refugial Eurosiberian species (e.g., *Taxus baccata* L., *Rhamnus alpina* L.) and marks the northern range limit for several Baetic endemics (e.g., *Genista longipes* Pau, *Vella spinosa* Boiss). The dominant shrubs are *Salvia lavandulifolia* subsp. *mariolensis* (Figuerola) Alcaraz & De la Torre, *Erinacea anthyllis* Link, and *Hormathophylla spinosa* L.; the debris is colonized by *Hedera helix* subsp. *rhizomatifera* McAll., grasses (*Festuca* L. spp., *Arrhenatherum* P. Beauv. spp.), and mosses.

Acipes alicantinus sp. nov. was also found in a scree slope in the Sierra de Mariola Natural Park, a rugged area spanning Alicante and Valencia provinces, formed by cretaceous limestone bedrock. Its highest peak, Montcabrer (1390 m a.s.l.), is the third highest in Alicante. The Mediterranean climate exhibits high microclimatic diversity, with frequent winter snow at higher elevations and significant cryptoprecipitation (fog, dew) in temperate seasons. This humidity supports relict flora, such as the "Micro-reserve of the Teixera d'Agres", which contains the southernmost *Taxus baccata* forest in Europe (Generalitat Valenciana 2006; Gualda Gómez 1988).

Remarks

Four individuals of *Acipes alicantinus* sp. nov. from Sierra de Aitana were previously recorded in the literature as *Acipes andalusius* by Enghoff & Reboleira (2013) and Jiménez-Valverde *et al.* (2015). The present records of *Acipes alicantinus* from Mont Cabrer, Cocentaina, 20 km apart from the type locality, represent a new, second locality of the species. These two sites are 250 km apart from the type locality of its closest relative, *Acipes andalusius* sp. nov.

Acipes andalusius Enghoff & Mauriès, 1999
Figs 7A–B, 10

Records in the literature

The species was described from 20 specimens collected in a cave in Peal del Becerro, Jaén, Spain (Enghoff & Mauriès, 1999), but the name of the cave (PB-2) was only mentioned later by Enghoff & Reboleira (2013). In this same publication they mentioned a personal communication from the collector, who stated that the species was also present in a nearby cave (PB-4). Eight further specimens were reported from collections made in the decade of 1990 by Mauriès (2013), five of them from the cave "Cueva de la Pasada de Algeciras", Hornachuelos, Córdoba, Spain, and three other specimens from "Pasada Jeira" (most probably misspelling of "Pasada de Algeciras", thus same locality).

Material examined

SPAIN • 1 ♂, 1 subadult ♂, 1 ♀; Jaén, Peal del Becerro, Cave PB-4, ca 400 m from entrance; 37°47′56.8″ N, 2°53′41.5″ W; 1010 m a.s.l.; 15 Aug. 1994; A. Tinaut leg.; UAH.

Remarks

The studied male specimen from PB-4 shows some minor differences from that of the original description from PB-2. The apical flange is less truncated and more rounded in its apical margin than shown in the drawing of the original description (Fig.10 C–D). The first pair of male legs was not drawn in the original description, but it is stated to be identical to those of *A. serratus*. However, in the studied specimen the first pair of legs is less modified, the tarsal remnant is slightly more developed and shows a visible terminal claw (Fig. 10F), not drawn in the original description of *A. serratus* (see Enghoff 1983: fig. 61). The specimens from Córdoba (Sierra Morena) were tentatively assigned to *Acipes* aff. *andalusius* by Mauriès (2013), but Reboleira & Enghoff (2017) considered them as *Acipes andalusius*.

Acipes bifilum Enghoff & Reboleira, 2013
Fig. 11A–B

Records in the literature

This species was described from two specimens collected from the cave "Gruta da Senhora", Moncarapacho, Algarve, Portugal (Enghoff & Reboleira 2013), and it is only known from the type series.

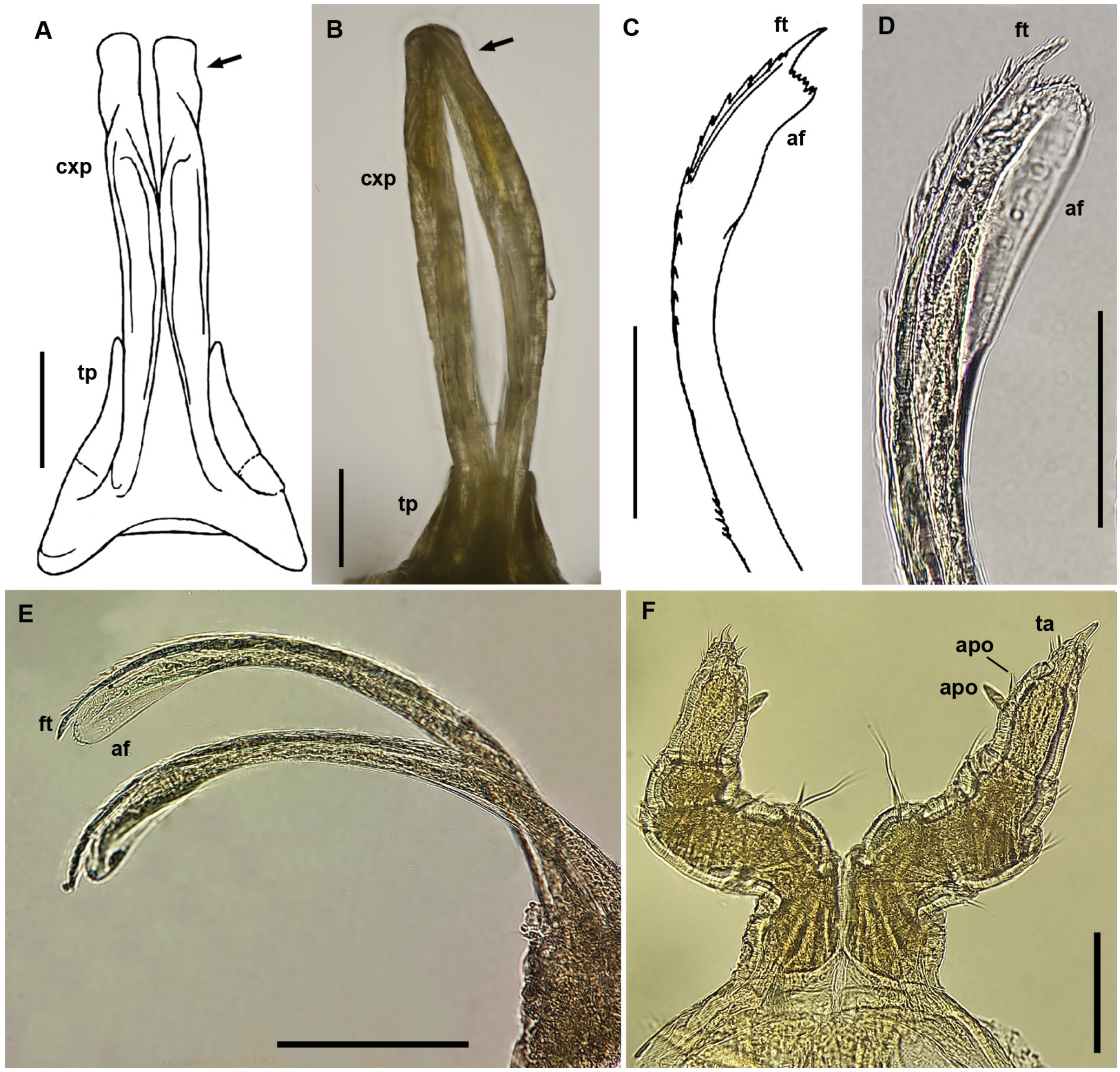

Fig. 10. Gonopods and first pair of male legs of *Acipes andalusius* Enghoff & Mauriès, 1999. **A**. Anterior gonopods in posterior view of specimen from PB-2, Jaén, redrawn from Enghoff & Mauriès (1999). Arrow indicating subapical emargination of coxal process. **B**. Anterior gonopods in posterior view of male specimen from PB-4, Jaén. UAH. Arrow indicating subapical emargination of coxal process. **C**. Distal part of posterior gonopods of specimen from PB-2, redrawn from Enghoff & Mauriès (1999). **D**. Tip of posterior gonopod of specimen from PB-4. UAH. **E**. Posterior gonopods in left lateral view of male specimen from PB-4. UAH. **F**. First pair of male legs of male specimen from PB-4. UAH. Abbreviations: *af* = apical flange; *apo* = tibial apophysis; *cxp* = coxal process; *ft* = filamentous tip; *ta* = tarsus remnant; *tp* = telopodite. Scale bars: A–C, E–F = 0.1 mm; D = 0.05 mm.

Remarks

Enghoff & Reboleira (2013) identified several morphological similarities between this species and *Acipes machadoi*, such as their high number of podous rings and their short anterior gonopod telopodites. Based on these traits and the geographical proximity of the two species, the authors suggested a potential close relationship between them. However, Enghoff & Reboleira (2013) also noted significant differences between the posterior gonopods of these two species (Fig. 11B–C). They also indicated that those of *A. bifilum* do not resemble those of any other species.

Acipes celtibericus Gilgado & Enghoff sp. nov.

urn:lsid:zoobank.org:act:9FF8003B-B3FC-4F07-8064-9552FF5F5B09
Figs 7D, 12–15

Diagnosis

Acipes celtibericus sp. nov. differs from the other *Acipes* species by the following combination of characters: at least four ommatidia per side (whereas *A. alicantinus* sp. nov., *A. andalusius, A. bifilum* and *A. machadoi* are anophthalmous; and *A. oligops* sp. nov. has only two or three), a developed accessory claw in the midbody legs (absent in *A. decolor* and *A. portosantoensis*), anterior gonopods with shallow subapical emargination (deep emargination in *A. atlanticus*), posterior gonopods with a filamentous tip (absent in *A. franzi* and *A lateralis*), and a truncate and serrulate flange (flange absent in *A. waldeni*, and lanceolate in *A. continentalis* and *A. serratus*).

Etymology

The specific epithet '*celtibericus*', refers to the pre-Roman people (Celtiberians) who inhabited the region of central Iberian Peninsula where this species was found, adjective.

Type material

Holotype

SPAIN • ♂; Burgos, Pineda de la Sierra, Sierra de Mencilla in Sierra de la Demanda, beech forest, MSS; 42°11′55″ N, 3°18′41″ W; 1470 m a.s.l.; 18 Jun. 2018 (trap set on 26 Jun. 2017); V.M. Ortuño, J.D. Gilgado and E. Ledesma leg.; MNCN 20.07/2106.

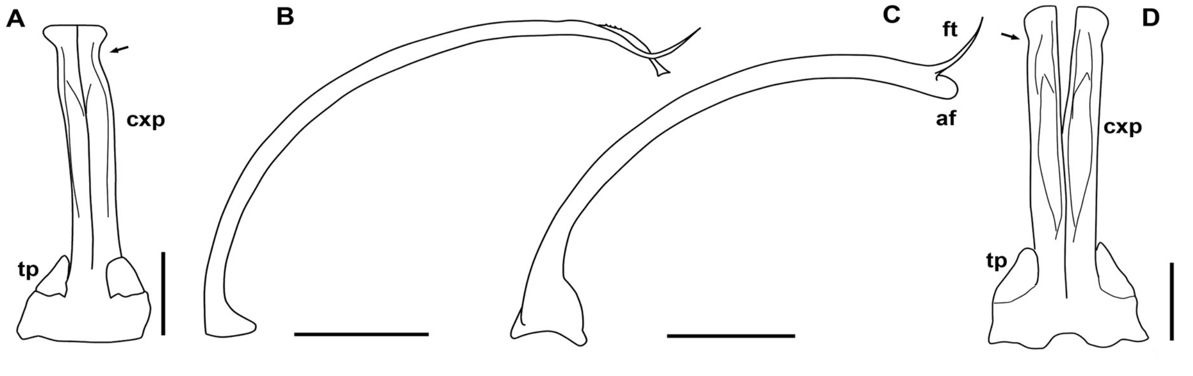

Fig. 11. Outline drawing of the gonopods of the cave species from Algarve, Portugal. Redrawn from Enghoff & Reboleira (2013). **A–B**. *Acipes bifilum* Enghoff & Reboleira, 2013. **A**. Anterior gonopods. Arrow indicates subapical emargination of coxal process. **B**. Posterior gonopods. **C–D**. *Acipes machadoi* Enghoff & Reboleira, 2013. **C**. Posterior gonopods. **D**. Anterior gonopods. Arrow indicatES subapical emargination of coxal process. Abbreviations: *af* = apical flange, *cxp* = coxal process, *ft* = filamentous tip, *tp* = telopodite. Scale bars: A, D = 0.01 mm; B–C = 0.05 mm.

Paratypes

SPAIN • 5 ♂♂, 5 ♀♀; same collection data as for holotype; MNCN 20.07/2107-2116 • 5 ♂♂, 5 ♀♀; same data as for preceding; UAH • 5 ♂♂, 5 ♀♀; same data as for preceding; 22 Jun. 2019 (trap set on 18 Jun. 2018); NHMD.

Other material examined

SPAIN • 33 ♂♂, 9 ♀♀, 8 juveniles; same collection data as for holotype; UAH • 333 ♂♂, 100 ♀♀, 21 juveniles; same data as for preceding; 22 Jun. 2019 (trap set on 18 Jun. 2018), UAH • 106 ♂♂, 37 ♀♀, 10 juveniles; same data as for preceding; 3 Aug. 2020 (trap set on 22 Jun. 2019); UAH • 1 ♂, 1 subadult ♂, 2 ♀♀, 1 juvenile; Pineda de la Sierra, Sierra de Mencilla in Sierra de la Demanda, Glaciar Circus, MSS in bare scree; 42°11′21″ N, 3°18′37″ W; 1750 m a.s.l.; 18 Jun. 2018 (trap set on 26 Jun. 2017); V.M. Ortuño, J.D. Gilgado and E. Ledesma leg.; UAH • 1 ♂, 1 ♀, 1 juvenile; same data as for preceding; 22 Jun. 2019 (trap set on 18 Jun. 2018); UAH • 1 ♀; Zaragoza, Añón de Moncayo, Moncayo Massif, Collado Bellido, MSS in bare Scree; 41°46′1″ N, 01°47′01″ W; 1540 m a.s.l.; 12 Dec. 2012 (trap set on 26 Sep. 2012); V.M. Ortuño, J.D. Gilgado, E. Ledesma and E. Cuesta leg.; NHMD • 1 ♂, 1 juvenile; same data as for preceding; 25 Mar. 2013 (trap set on 12 Dec. 2012); NHMD • 1 ♂; same data as for preceding; 12 Mar. 2014 (trap set on 23 Oct. 2013); UAH.

Description

Pale brown to dark amber colour in preserved specimens (Figs 7D, 12A–B). Males 10.5–12.5 mm long, and 0.52–0.63 mm in maximum ring vertical diameter, with 35–38 podous rings including collum + 2 apodous rings + telson. Measures taken on 10 randomly chosen males. Females 11.5–14.5 mm long, and 0.58–0.73 mm in maximum height, with 38–40 podous rings including collum + 2 (1) apodous rings + telson. Measures taken on 10 randomly chosen females.

HEAD. Males with parrot beak modification of cardo and stipes (Fig. 12A–D). Labrum with 3 teeth and 6+6 labral and 2+2 supralabral setae (Fig. 12D–F). Cephalic capsule with several smaller setae laterally, 1+1 setae on frons, and 1+1 long setae on vertex (Fig. 12A–C, E). One row of 4–6 blackish ommatidia (Fig. 12A), but some can be displaced (poorly visible on SEM (Fig. 12C). Antenna with antennomere 5 with a distal ring of thick sensilla basiconica, antennomere 6 with half such ring (sensilla absent ventrally), and antennomere 7 with a dorsodistal row of shorter sensilla basiconica (Fig. 12C, E). Antennomere lengths (mm): 0.05, 0.17, 0.16, 0.13, 0.16, 0.13, 0.05, 0.04.

TRUNK. Collum with 4+4 setae (Fig. 12C). Second ring with 4+4 setae, increasing up to 12+12 long setae on the last rings of the body (Figs 12C, 15C, E). Length of midbody setae around 18% of midbody ring height. Around 10 striae in ventral half of the rings. Telson: epiproct with 2+2 long dorsal, 1+1 lateral, and 1+1 ventral setae. Hypoproct with 1+1 setae, and paraprocts with 2 setae each (Fig. 15E).

LEGS. First pair of legs modified (Fig. 13A). Tibiae of first pair of legs of male robust, twice as long as wide, and with two curved, tusk-like apophyses, the proximal one larger than the distal one. Tarsus remnant visible, with terminal claw present. All legs of males, except in posteriormost third of body, with lanceolate, transversely striate setae on femur (2), postfemur (2) and tibia (2) (Fig. 13B, D). Number of lanceolate setae decreasing towards and after midbody legs. Lanceolate setae absent in females. Accessory claw visible in midbody legs (Fig. 13D).

ANTERIOR GONOPODS. Coxal processes (*cxp*) with shallow subapical emargination, telopodites (*tp*) slightly more than a third of the length of coxal processes. Distal part of coxal processes more acute in type locality (Fig. 14A–C) than in the specimens from Moncayo Massif (Fig. 15A).

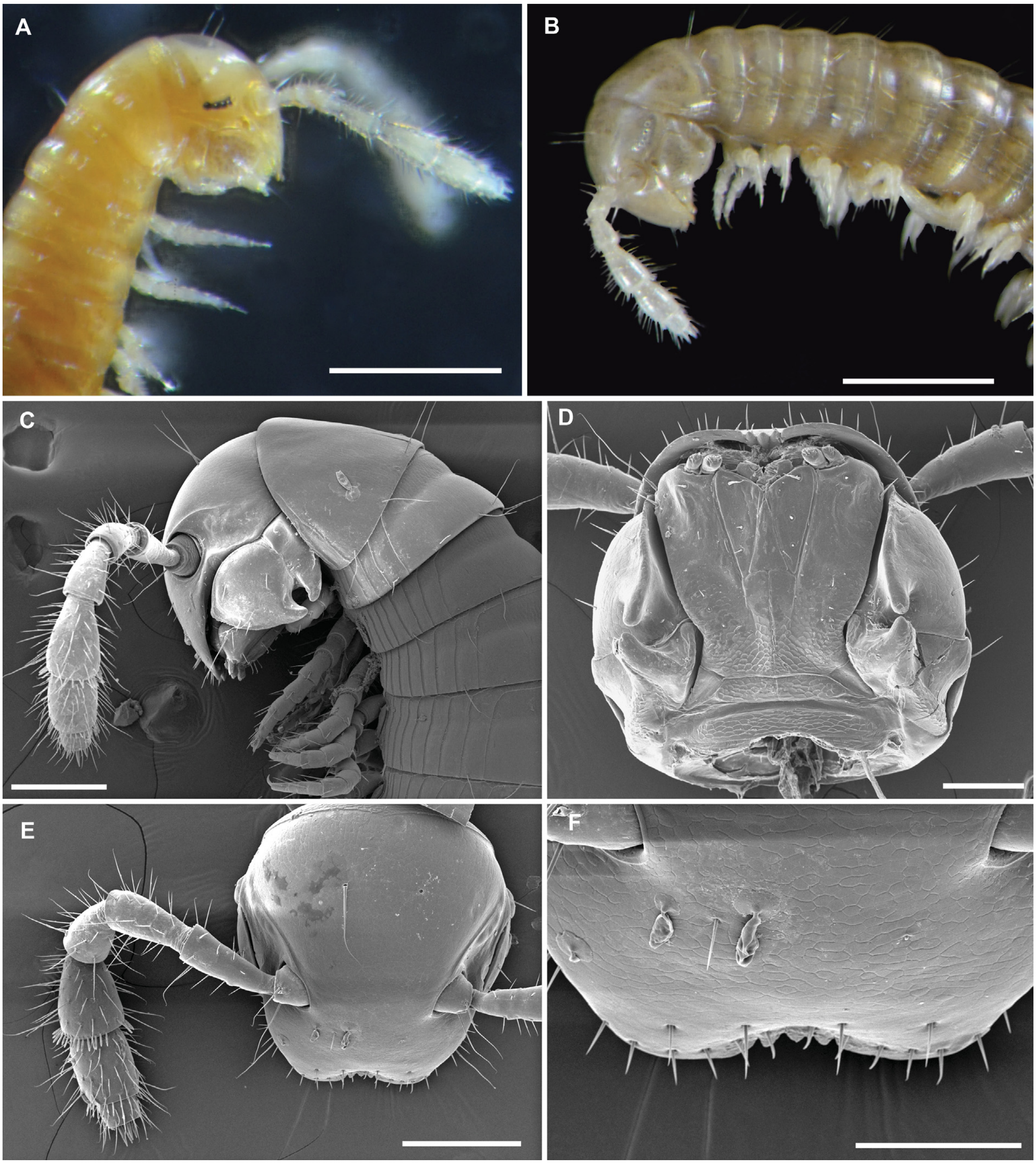

Fig. 12. Head and first rings of male specimens of *Acipes celtibericus* sp. nov. Gilgado & Enghoff from Mencilla, Sierra de la Demanda, Burgos. **A**. Specimen from same locality and capture as holotype, in alcohol. Right lateral view. UAH. **B**. Same specimen, dry, in left lateral view. UAH. **C**. Specimen from same locality and capture as holotype. Head and first rings in left lateral view. UAH. **D**. Another specimen from same locality and capture as holotype. Head in ventral view. UAH. **E**. Another specimen from same locality and capture as holotype. Head in dorsofrontal view. UAH. **F**. Detail of labrum and prelabral setae of same specimen as in E. Scale bars: A–B, D = 0.5 mm; C, E = 0.2 mm; F = 0.1 mm.

Posterior gonopods. Curved, distal part anteriorly serrulate, including a relatively long filamentous tip (*ft*), and a truncate apical flange (*af*) serrulate in its apical margin (Figs 14C, E–F, 15B).

Type locality

The Sierra de Mencilla, in the northwestern Sierra de la Demanda (Burgos, Spain), reaches 1932 m a.s.l. at Pico Mencilla. It is composed mainly of Paleozoic slates, quartzitic sandstones, and conglomerates (Fuentes Cabrera 1981). Its morphology is asymmetrical: the southern slopes descend smoothly towards the Arlanzón valley, while the northern slopes are steep and host large block fields and colluvial cones such as "La Concha" (Fuentes Cabrera 1981). During the Quaternary, small glaciers developed on its northern side, leaving cirques and moraines around Pineda de la Sierra. Cosmogenic dating has shown that fossil debris-covered glaciers on the northern slope of Mencilla persisted from the Last Glacial Maximum (~17.8 ka) to the Oldest Dryas (~16.5 ka), and possibly survived into the Holocene under protective debris mantles (Fernández-Fernández *et al*. 2017). The climate is cold and continental montane, with annual precipitation ranging between 700 and 1200 mm depending on altitude, and frequent snowfall in winter (Fuentes Cabrera 1981). Biogeographically, the Sierra de Mencilla lies at the interface of Eurosiberian and Mediterranean sectors, which enhances species diversity. Forests of Pyrenean oak (*Quercus pyrenaica* Willd.) dominate mid-elevations, with beech (*Fagus sylvatica* L.) on humid north-facing slopes, while higher zones support Scots pine (*Pinus sylvestris* L.), heathlands, and montane grasslands (Fuentes Cabrera 1981).

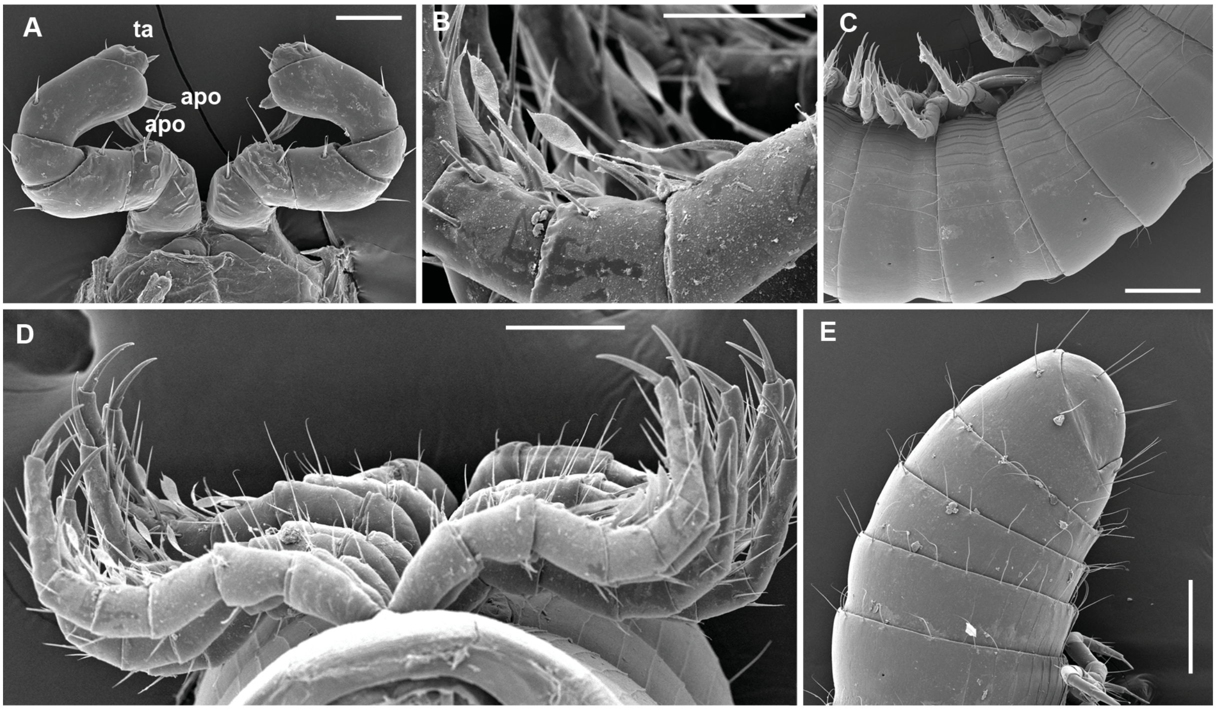

Fig. 13. Details of the legs, trunk and telson of a male specimen of *Acipes celtibericus* Gilgado & Enghoff sp. nov. from Mencilla, Sierra de la Demanda, Burgos. **A**. First pair of legs in posterior view. Same specimen as in Fig. 12D. **B**. Detail of postgonopodal legs and lanceolate setae of same specimen in anterior view. **C**. Trunk of gonopodal and surrounding rings in lateral view. Same specimen as in Fig. 12C. **D**. Postgonopodal legs in anterior view. Same specimen as in Fig. 12D. **E**. Posterior-most body rings of trunk and telson in left lateral view. Same specimen as in Fig. 12C. Abbreviations: *apo* = tibial apophysis, *ta* = tarsus remnant. Scale bars: A–B = 0.05 mm; C, E = 0.02 mm; D = 0.1 mm.

Acipes celtibericus sp. nov. was also found in bare scree on the northern slope of the Moncayo Massif. This mountain is the highest peak of the Iberian System (2314 m a.s.l.), and it is located between the provinces of Zaragoza (Aragón) and Soria (Castilla y León). Its geology is characterized by siliceous materials, including angular blocks of Mesozoic and Palaeozoic quartzites and sandstones fractured by ice, accumulated through solifluction processes during the cold periods of the Quaternary (Pellicer 1980). The climate is temperate and humid, with notable differences between slopes: the northern slope, wetter due to interception of Atlantic fronts via the Ebro valley, supports forests typical of Atlantic

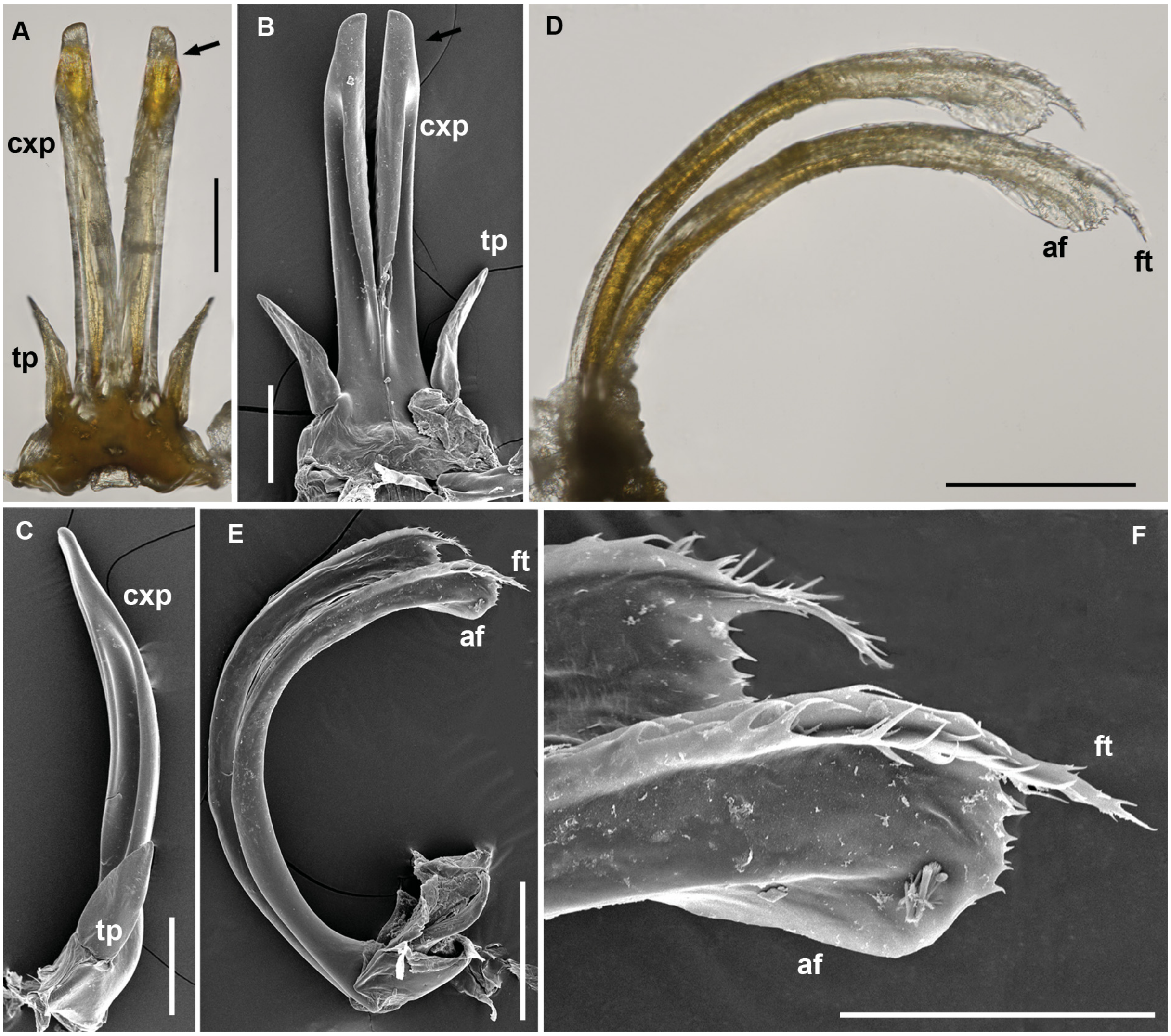

Fig. 14. Gonopods of *Acipes celtibericus* Gilgado & Enghoff sp. nov. from Mencilla, Sierra de la Demanda, Burgos. **A**. Anterior gonopods of holotype in posterior view. MNCN 20.07/2106. Arrow indicates subapical emargination of coxal process. **B**. Anterior gonopods of specimen from same locality and capture as holotype in posterior view. UAH. Arrow indicates subapical emargination of coxal process. **C**. Anterior gonopods of another specimen from same locality and capture as holotype left lateral view. UAH. **D**. Posterior gonopods of holotype in right lateral view. MNCN 20.07/2106. **E**. Posterior gonopods of another specimen from same locality and capture as holotype left lateral view. UAH. **F**. Detail of the distalmost part of same gonopods as E. Abbreviations: *af* = apical flange; *cxp* = coxal process; *ft* = filamentous tip; *tp* = telopodite. Scale bars: A–E = 0.1 mm; F = 0.05 mm.

climates, contrasting with the surrounding Mediterranean environment, making Moncayo an "Atlantic island" (Ballarín 1985; Navarro 1989). Annual precipitation exceeds 1000 mm on the wetter slopes, sustaining diverse vegetation including trees such as European beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*), and black pine (*Pinus uncinata* Ramond ex A.DC.), even on stony screes at 1540 m a.s.l. where soil is scarce (Ballarín 1985; Navarro 1989).

Remarks

Acipes celtibericus sp. nov. was found in two mountains of the Iberian System, 130 km apart (Fig. 6). While the posterior gonopods in both populations are identical, the coxal apophysis of anterior gonopods of males from Moncayo Massif shows a more rounded distal part after the subapical emargination (Fig. 14A), similar to that of *A. continentalis* (Fig. 16C). This species has so far only been found in the MSS, but its presence in surface environments, including soil or deeper soil layers, cannot be discarded. The two populations were discovered in different macrohabitats. In the Mencilla Mountain, the species was significantly more abundant in a beech forest at 1470 m a.s.l. than in bare scree at 1750 m a.s.l.. However, in the Moncayo Massif, it was exclusively found in bare scree at 1540 m a.s.l., with no individuals captured in the beech forest at 1420 m a.s.l.

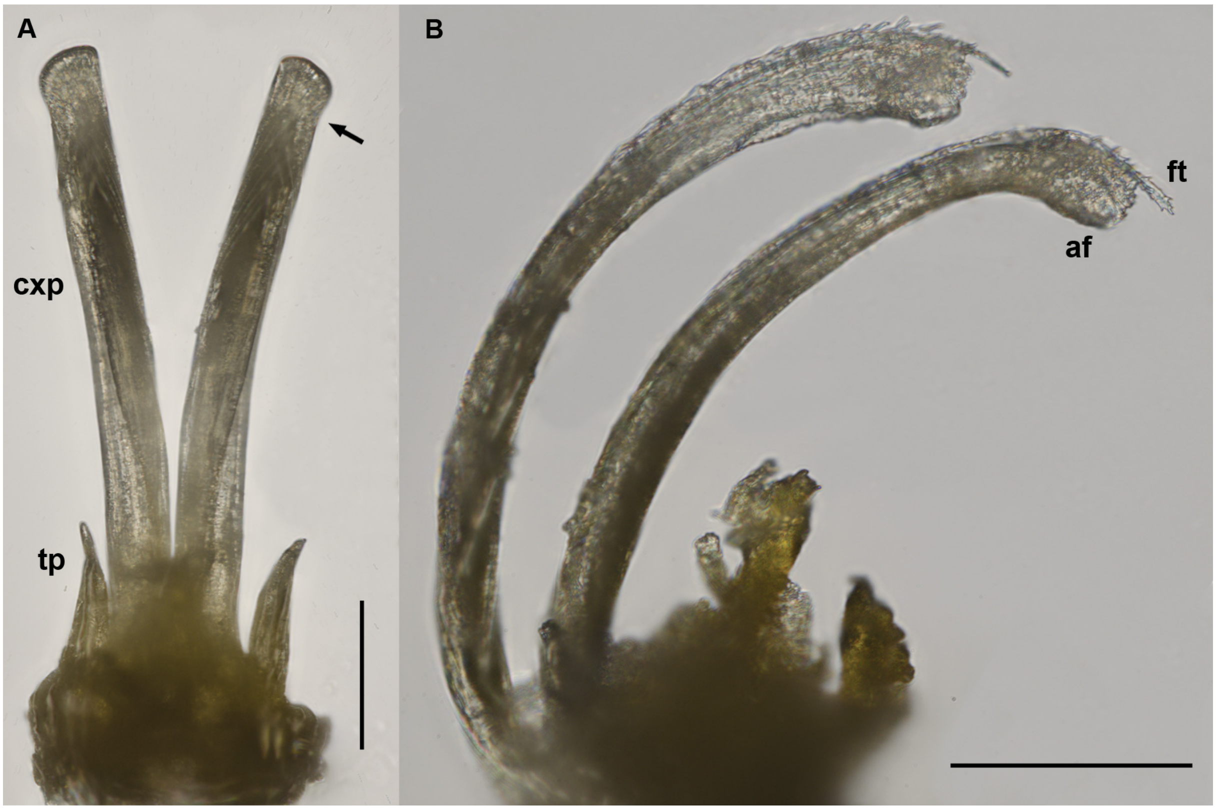

Fig. 15. Gonopods of *Acipes celtibericus* Gilgado & Enghoff sp. nov. From Moncayo Massif, Zaragoza. UAH. **A**. Anterior gonopods in posterior view. Arrow indicates subapical emargination of coxal process. **B**. Posterior gonopods in right lateral view. Abbreviations: *af* = apical flange, *cxp* = coxal process, *ft* = filamentous tip, *tp* = telopodite. Scale bar = 0.1 mm.

Acipes continentalis Enghoff, 1986
Figs 7E, 16

Records in the literature

This species was originally described from a single specimen collected at the “Pico” mountain pass (“Puerto del Pico”), located in Cuevas del Valle, Sierra de Gredos, Ávila, Spain (Enghoff 1986). Years later, Enghoff & Mauriès (1999) examined 59 specimens collected during the 1960s and reported the presence of the species in the Sierra de Guadarrama, in the Navacerrada Mountain Pass, Cercedilla, and close to this locality in Peñalara Mountain, both in Madrid, Spain.

Material examined

Other material

SPAIN • 1 ♂; Madrid, Cercedilla, Schmidt trail, deadwood; 40°47′15″ N, 4°03′02″ W; 1830 m a.s.l.; 27 Mar. 2017; E. Recuero leg.; UAH • 1 ♂; Madrid, La Cabrera, cleared forest of *Quercus ilex*; 40°51′25.32″ N, 3°37′19.25″ W; 1030 m a.s.l.; 27 Dec. 2020; D. Cabanillas leg.; UAH • 1 ♀; Madrid, Rascafría, Sierra de Guadarrama National Park (henceforth SGNP), Alto de los Poyales, MSS; 40°53′40.48″ N, 3°56′10.13″ W; 1890 m a.s.l.; 14 Oct. 2016 (trap set on 9 Jun. 2016); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; UAH. • 1 ♀; Madrid, Rascafría, SGNP, Scree, between peaks Cabeza de Hierro Mayor and Cabeza de Hierro Menor, MSS; 40°47′54.79″ N, 3°56′6.45″ W; 2300 m a.s.l.; 14 Oct. 2016 (trap set on 9 Jun. 2016); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; UAH. • 1 ♀, 1 juvenile; Madrid, Cercedilla, SGNP, Cerro Ventoso, Scree, MSS; 40°47′28.83″ N, 4° 3′24.32″ W; 1870 m a.s.l.; 17 Sept. 2015 (trap set on 9 Jun. 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; NHMD • 1 ♀; same data as for preceding; 21 Sept. 2016 (trap set on 9 Jun. 2016); UAH • 3 ♂♂; Madrid, Rascafría, SGNP, Collado de Valdemartín, Scree, MSS; 40°47′43.48″ N, 3°57′20.81″ W; 2155 m a.s.l.; 6 Nov. 2015 (trap set on 3 Jul. 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; NHMD • 2 ♂♂; Madrid, Rascafría, SGNP, Collado de la Flecha, La Gelecha, Scree, MSS; 40°55′25.95″ N, 3°55′16.92″ W; 1865 m a.s.l.; 9 Jun. 2016 (trap set on 6 Oct. 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; UAH • 1 ♀; Madrid, Manzanares el Real, SGNP, La Maliciosa, Collado del Piornal, scree, MSS; 40°46′17.26″ N, 3°58′16.14″ W, 2100 m a.s.l.; 22 Sep. 2015 (trap set on 9 Jun. 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; NHMD • 1 ♂; same data as for preceding; 26 May 2016 (trap set on 22 Sept. 2015); UAH • 1 ♂, 2 ♀♀; Segovia, Real Sitio de San Ildefonso, SGNP, Falda del Cerro de la Muela, Cancho del Río Peces, MSS; 1605 m a.s.l.; 17 Sept. 2015 (trap set on 20 May 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; NHMD • 7 ♂♂, 23 ♀♀; same as for preceding; 1 May 2016 (trap set on 17 Sept. 2015); UAH • 1 ♂, 15 ♀♀; same data as for preceding; 21 Sep. 2016 (trap set on 1 May 2016); UAH • 1 juvenile; Segovia, Real Sitio de San Ildefonso, SGNP, Falda del Montón de Trigo, Corrales de la Majada Minguete; MSS; 40°47′45.00″ N, 4°03′57.98″ W; 1820 m a.s.l.; 17 Sep. 2015 (trap set on 20 May 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; NHMD • 7 ♂♂, 11 ♀♀; same data as for preceding; 26 May 2016 (trap set on 17 Sep. 2015); UAH • 1 ♀; same data as for preceding; 21 Sep. 2016 (trap set on 26 May 2016); UAH • 7 ♂, 2 ♀♀; Segovia, Real Sitio de San Ildefonso, SGNP, Loma del Noruego, Canchal de La Pedriza, MSS; 40°48′52.12″ N, 3°58′20.87″ W; 1790 m a.s.l.; 22 Sep. 2016 (trap set on 1 May 2016); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; UAH • 1 ♀, 1 juvenile; Segovia, Navafría, SGNP, Pine forest beside Navafría shelter, MSS (buried pitfall trap); 40°59′12.92″ N, 3°48′51.60″ W; 1780 m a.s.l.; 22 Sep. 2015 (trap set on 24 Jun. 2015); V.M. Ortuño, J.D. Gilgado, E. Ledesma *et al.* leg.; NHMD • 5 ♂♂, 2 ♀♀; same data as for preceding; 13 Jun. 2016 (trap set on 22 Sep. 2015); UAH • 1 ♂, 1 ♀; same data as for preceding; 40°59′12.84″ N, 3°48′52.57″ W; UAH.

Remarks

This species seems to have a relatively wide elevational range, from 930 to 2300 m a.s.l., and is found in surface habitats, under stones and in deadwood, and MSS. This species has been recorded in Sierra de Gredos (holotype) and Sierra de Guadarrama mountain ranges, and the new records indicate that it might be widespread in the latter (Fig. 6). The type specimens of *A. continentalis* from Gredos and the specimens from Guadarrama (100 km distance) also show some differences according to Enghoff & Mauriès (1999), such as the different development of the terminal claw of the modified first pair of legs of the male in the Guadarrama specimens, apical flange (*af*) protruding parallel to the filamentous tip (Fig. 16A–B, D–E), and apical flange of Guadarrama specimens without spines (but spines can be observed under SEM, Fig. 16E). Enghoff (1986) already questioned that this developed claw in the first leg pair of the holotype could be an individual aberration; however, more material from the type locality should be examined to test it.

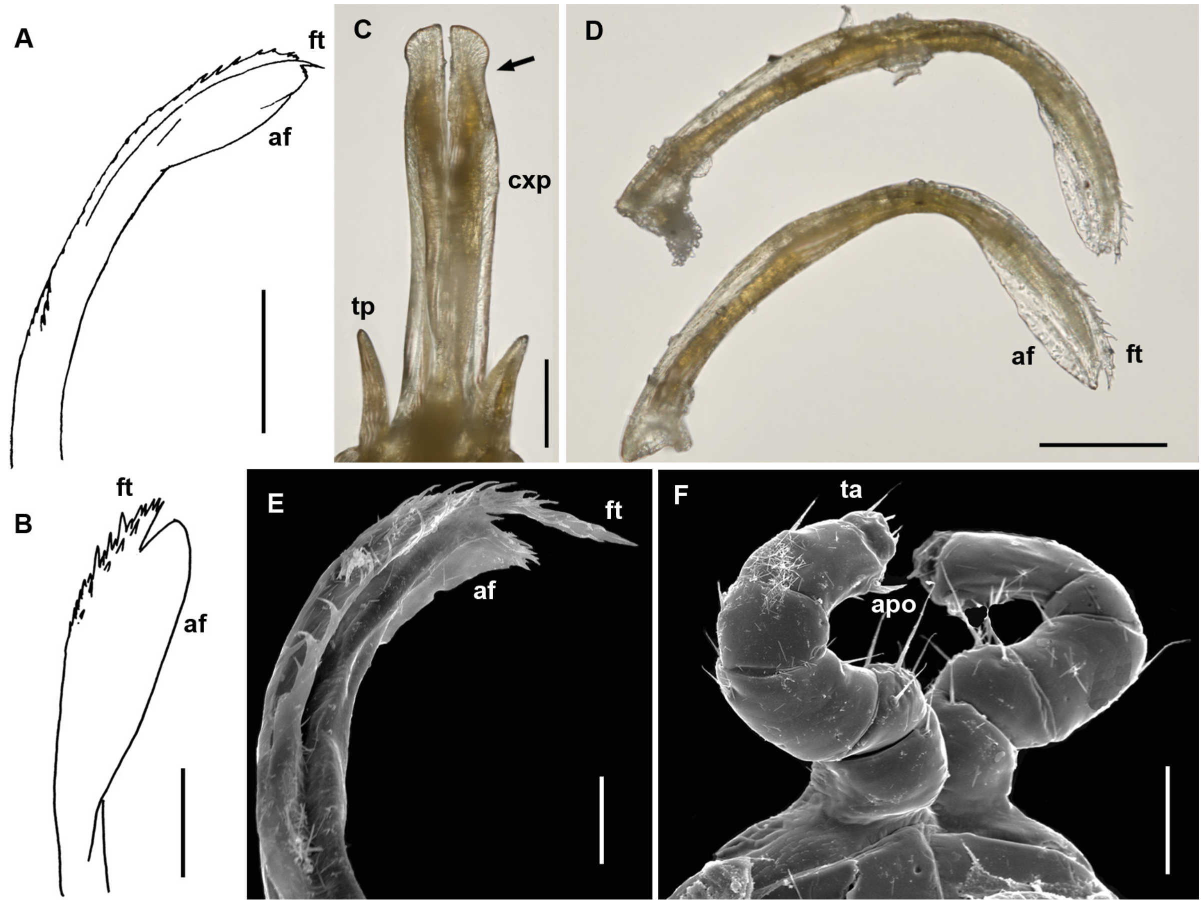

Fig. 16. Gonopods and first leg pair of male of *Acipes continentalis* Enghoff, 1986. **A**. Distal part of posterior gonopod of *A. continentalis* from Sierra de Gredos, Ávila, redrawn from Enghoff (1986). **B**. Tip of posterior gonopod of *A. continentalis* from Sierra de Guadarrama, Madrid, redrawn from Enghoff and Mauriès (1999). **C**. Anterior gonopods of *A. continentalis* from Rascafría, Sierra de Guadarrama in posterior view. UAH. Arrow indicates subapical emargination of coxal process. **D**. Posterior gonopods of *A. continentalis* from Sierra de Guadarrama, from same specimen, in right lateral view. Note that the gonopods were bent during manipulation for taking the photographs. **E**. Tip of posterior gonopod in dorsolateral view of specimen from Guadarrama, different specimen. NHMD. **F**. Modified first pair of legs of male in anterior view, same specimen as E. Abbreviations: *af* = apical flange, *apo* = tibial apophysis, *cxp* = coxal process, *ft* = filamentous tip, *ta* = tarsus remnant, *tp* = telopodite. Scale bars: A, C–D = 0.1 mm; B, F = 0.05 mm; E = 0.02 mm.

Acipes machadoi Enghoff & Reboleira, 2013

Fig. 11C–D

Records in the literature

This species is known only from one male specimen which was captured in the cave "Gruta do Vale Telheiro", Loulé, Algarve, Portugal (Enghoff & Reboleira 2013).

Remarks

This is the largest species of *Acipes*, both in size and number of rings (Enghoff & Reboleira 2013).

Acipes oligops Gilgado & Enghoff sp. nov.

urn:lsid:zoobank.org:act:84E0CD53-129F-4EAB-B4F9-D7FA7F2A72A0

Figs 7F, 17

Diagnosis

Acipes oligops sp. nov. differs from *A. andalusius*, *A. alicantinus* sp. nov., *A. bifilum*, and *A. machadoi* by the presence of ommatidia, and from the other eyed species of *Acipes* by having only two to three ommatidia on each side of the head (vs 4–15 in A. *atlanticus*, 4–6 in *A. celtibericus* sp. nov., 5–8 in *A. continentalis*, 5–9 in *A. decolor*, 6–8 in *A. franzi*, 6–9 in *A. lateralis*, 5–10 in *A. portosantoensis*, 4–9 in *A. serratus*, and 4–12 in *A. waldeni*).

Acipes oligops sp. nov. further differs from all these species by the unique shape of the first pair of legs of the male (except *A. decolor* which is known only from females), with a single stout, claw-like tibial apophysis, vs apophysis absent in *A. machadoi*; apophysis narrow in *A. portosantoensis*; two apophyses in *A. alicantinus* sp. nov., *A. andalusius*, *A. atlanticus*, *A. bifilum*, *A. celtibericus* sp. nov., *A. continentalis*, *A. franzi*, *A. serratus*, and *A. waldeni*; apophysis similar in proportions to *A. lateralis*, but the latter having a prominent tarsus, vs. almost absent in *A. oligops* sp. nov.

Moreover, *Acipes oligops* sp. nov. differs from other species in gonopod shape (except *A. decolor*, male unknown): posterior gonopod with a filamentous tip and a lanceolate flange, serrulate in its distalmost part (filamentous tip absent in *A. franzi* and *A. lateralis*; flange absent in *A. bifilum* and *A. waldeni*; flange smooth in *A. atlanticus*, *A. machadoi*, and *A. serratus*; flange clearly truncated in *A. celtibericus* sp. nov. and *A. portosantoensis*, truncated or rounded in *A. andalusius*); anterior gonopod with a very slender coxal apophysis with a slight subapical emargination leaving a rounded distalmost part narrower than the rest of the coxal process (marked emargination but distalmost part as wide as the rest of coxal process in *A. continentalis*; almost no emargination and distalmost part not rounded in *A. alicantinus* sp. nov.).

Etymology

The specific epithet (Greek) means 'few eyes' and refers to the low number of ommatidia. Noun in apposition.

Type material

Holotype

SPAIN • ♂; Guadalajara, Tamajón, Sierra del Ocejón, Arroyo de Valdelapuerta, MSS (alluvial); 41°1′20″ N, 3°15′1″ W; 1050 m a.s.l.; 9 Jun. 2013 (trap set on 11 Oct. 2012); J.D. Gilgado and V.M. Ortuño leg.; NHMD 1184664.

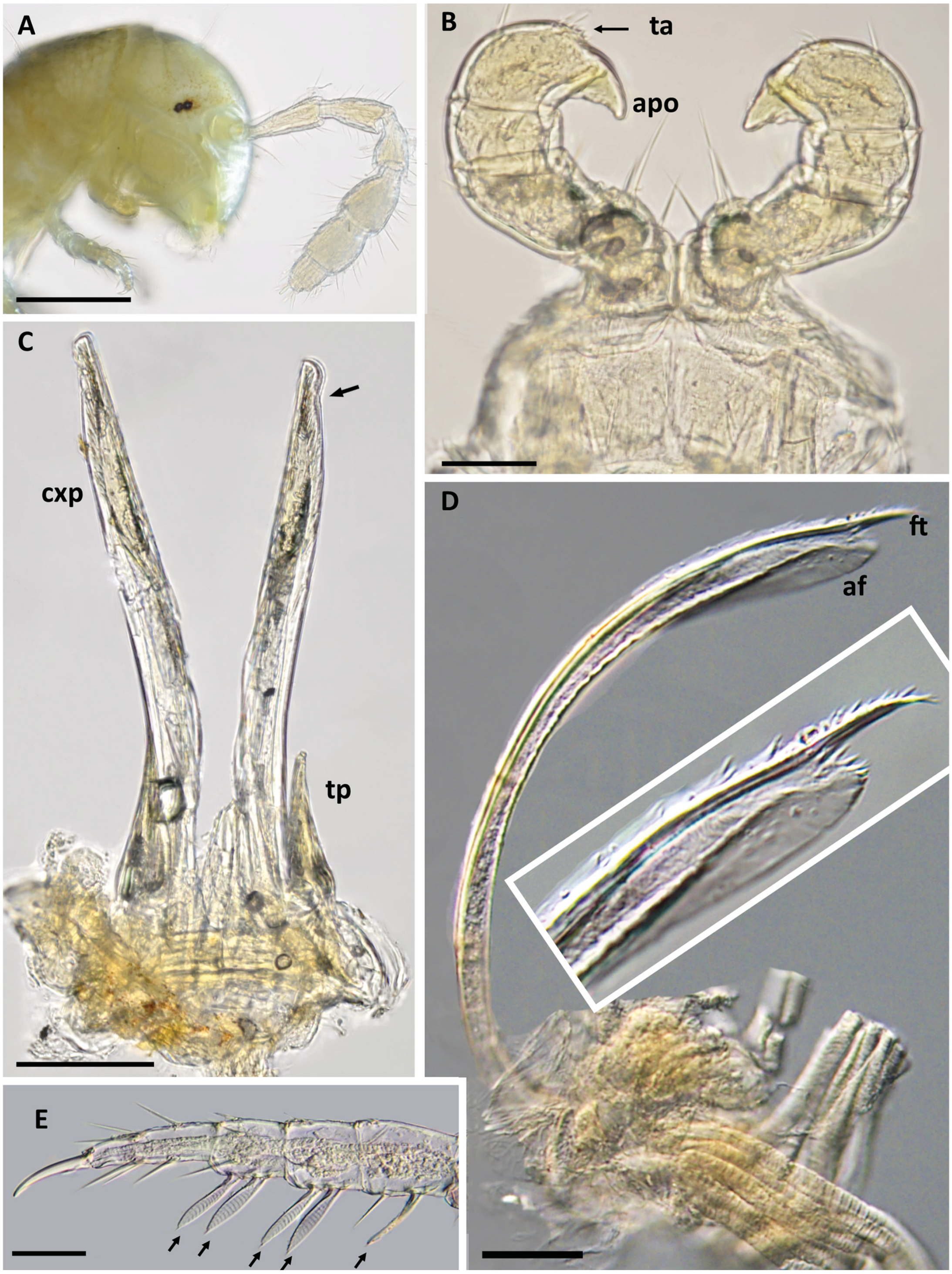

Fig. 17. *Acipes oligops* Gilgado & Enghoff sp. nov. **A–C**. Paratype male. MNCN 20.07/2167. **D–E**. Holotype male. NHMD 1184664. **A**. Head, antenna, and first two legs in right lateral view). **B**. First pair of legs in posterior view. **C**. Anterior gonopods in posterior view. Arrow indicates subapical emargination of coxal process. **D**. A posterior gonopod in right lateral view, inset: distalmost part enlarged. **E**. A pregonopodal leg (arrows point at lanceolate setae). Abbreviations: *af* = apical flange, *apo* = tibial apophysis; *cxp* = coxal process, *ft* = filamentous tip, *tp* = telopodite. Scale bars: A = 0.5 mm; B, D–E = 0.05 mm; C = 0.1 mm.

Paratype

SPAIN • 1 ♂; same locality as for holotype but under a stone on the surface of a temporal watercourse; 16 Mar. 2024; J.D. Gilgado and V. Martínez-Pillado leg.; MNCN 20.07/2167.

Description

Little to no pigmentation, whitish, ivory to amber colour (Figs 7F, 17A). Females unknown, description based on two males. Measurements: 7.6–8.7 mm; midbody vertical diameter 0.36–0.4 mm. 34–39 podous rings including collum + 1–3 apodous rings + telson.

HEAD (FIG. 17A). Males with parrot beak modification of cardo and stipes. Labrum with 3 teeth and 5+5 labral and 2+2 supralabral setae. Cephalic capsule with 1+1 setae on frons, and 1+1 long setae on vertex. Two clearly separated black ommatidia on each side of the head (three on left side in paratype) (Fig. 17A). Antenna with antennomere 5 with a distal ring of thick sensilla basiconica, antennomere 6 with half such ring (sensilla absent ventrally), and antennomere 7 with a dorsodistal row of shorter sensilla basiconica. Antennomere lengths (mm): 0.08, 0.38, 0.30, 0.24, 0.31, 0.25, 0.11, 0.05.

TRUNK. Collum with 4+4 setae. Midbody rings with 8+8 setae, increasing up to 10 + 10 on the last rings of the body. Length of midbody setae around 16–23% of midbody ring height, setae longest on anterior part of body. Seven to eight visible striae in ventral half of the rings. Telson: epiproct with 2+2 long dorsal, 1+1 lateral, and 1+1 ventral setae. Hypoproct with 1+1 setae, and paraprocts with 2 setae each.

LEGS. First pair modified (Fig. 17B). Stout, podomeres distinct; prefemur, femur, postfemur and tibia forming a curved limb terminating in a very stout, claw-like tibial apophysis (*apo*); tarsus remnant (*ta*) tiny, with several spikes. All legs, except in posteriormost part of body, with up to five lanceolate, transversely striate setae on femur (1), postfemur (2) and tibia (2) (Fig. 17E, arrows). Accessory claw strongly reduced but present in midbody legs (Fig. 17E).

ANTERIOR GONOPODS (FIG. 17C). Very slender coxal processes (*cxp*) (12 times as long as wide) with only slight subapical lateral emarginations leaving a rounded distalmost part narrower than the rest of coxal process, and very slender telopodites (*tp)*. Telopodites approximately ¼ of the length of coxal processes.

POSTERIOR GONOPODS (FIG. 17D). slender and curved, with a long, slender, spinose filamentous tip (*ft*) and a lanceolate apical flange (*af)* with a serrulate distal margin.

Type locality

The temporary watercourse of the Arroyo de Valdelapuerta in Tamajón, Guadalajara, is a narrow streambed carved into a calcareous environment but composed mainly of slates. The area is renowned for its distinctive geomorphological features, most notably extensive karstified formations of the Ciudad Encantada type, developed on Cretaceous dolomites and limestones (Carcavilla *et al*. 2025). According to the Köppen climate classification, the Tamajón region has a temperate, dry continental climate, intermediate between arid and humid conditions (Rivas Goday & Esteban 1944). It is characterized by long, harsh winters, with mean annual temperatures ranging from 9 to 14°C and pronounced thermal amplitudes. Frosts are frequent, and precipitation is scarce, typically between 350 and 600 mm per year. From a biogeographic perspective, the site lies within a transitional zone between the Mediterranean Iberian and Celtiberian-Alcarrean sectors (Rivas Martínez 1987). Vegetation in the gully surrounding the stream consists mainly of *Juniperus thurifera* L. and *Quercus ilex* L., with scattered *Juniperus oxycedrus* L., basophilic scrub (lavender, thyme, etc.), and several rupicolous and sub-rupicolous species growing on the rocky outcrops (de la Fuente García 1982).

Remarks

Acipes oligops sp. nov. seems to be closely related to *A. continentalis* and *A. celtibericus* sp. nov., but its two known specimens show the same distinct combination of characters that warrant its recognition as a new species (small size, low number of ommatidia, and especially the unique shape of the first pair of legs). The location and habitat (lithology, vegetation, elevation, etc.) are also different from those known for *A. continentalis* and *A. celtibericus* sp. nov. The **s**hape of the first pair of legs in males clearly differs from all other *Acipes* species, being most similar to *A. portosantoensis* Enghoff, 1983, but with much stouter tibial apophysis.

Key to the species of *Acipes*

Based in part on the keys in Enghoff (1983). The key refers to adult males, and the used characters refer to the gonopods when nothing else is mentioned, except in the case of *A. decolor* of which the male is unknown. A country in square brackets indicates that the species does not occur in the Iberian region.

1. Without ommatidia 2
– With ommatidia 5

2. Filamentous tip very long, smooth; apical flange long, slender, smooth (Fig. 11B). PORTUGAL: Algarve .... ***A. bifilum*** Enghoff & Reboleira, 2013
– Apical flange not long and slender 3

3. Filamentous tip of posterior gonopods very long, almost smooth (Fig. 11C); first pair of legs not hook-like; body vertical diameter 0.98 mm, 83 podous body rings. PORTUGAL: Algarve .... ***A. machadoi*** Enghoff & Reboleira, 2013
– Filamentous tip shorter; first pair of legs strongly curved, hooklike; body vertical diameter max. 0.71 mm, max. 61 podous rings 4

4 Tibiae of first pair of legs of male slender, more than twice as long as wide; subapical emargination of coxal process of anterior gonopods subtle, distalmost part of anterior gonopods narrower than prior to the emargination; flange of posterior gonopods lanceolate; accessory claw not visible on midbody legs. SPAIN: Alicante (Baetic System)........................ ***A. alicantinus*** Gilgado & Enghoff sp. nov.
– Tibiae of first pair of male legs around 1.5 times as long as wide; coxal process of anterior gonopods of equal width along all its length, flange of posterior gonopods truncate or rounded, accessory claw of midbody legs visible. SPAIN: Jaén, Córdoba (Sierra Morena, Baetic System) .... ***A. andalusius*** Enghoff & Mauriès, 1999

5. Two or three ommatidia on each side of the head. First pair of legs regularly curved, smooth, with a single claw-like apical tibial apophysis (Fig. 17B). SPAIN: Guadalajara (Central System) .... ***A. oligops*** Gilgado & Enghoff sp. nov.
– At least four ommatidia on each side of the head. First pair of male legs different 6

6. Length of metazonital setae of midbody rings circa 5% of body vertical diameter (Enghoff 1983: fig. 19); body unpigmented. (Male unknown). [PORTUGAL:] Madeira .. ***A. decolor*** Enghoff, 1983
– Length of metazonital setae at least 7% of body vertical diameter, usually much longer 7

7. Posterior gonopods much longer than anterior ones, curved in three dimensions, without an apical flange. (Enghoff 1983: figs 67–69, 73). [PORTUGAL]: Madeira .... ***A. waldeni*** Enghoff, 1983
– Posterior gonopods shorter, with an apical flange 8

8. Flange of posterior gonopod directed laterad, no filamentous tip (Enghoff 1983: figs 87–88). [PORTUGAL]: Madeira .... ***A. lateralis*** Enghoff, 1983
– Flange of posterior gonopod directed dorsad, usually a shorter or longer filamentous tip 9

9. Posterior gonopod without a filamentous tip (Enghoff 1983: figs 92–93). Length of metazonital setae of midbody rings 28–37% of body vertical diameter (Enghoff 1983: fig. 20). [SPAIN]: Canary Islands .... ***A. franzi*** (Loksa, 1967)
– Posterior gonopod with a shorter or longer filamentous tip 10

10. Length of metazonital setae of midbody rings 7–9% of body vertical diameter (Enghoff 1983: fig. 17); metazonites rough due to dense coverage of tiny (< 0.01 mm) bumps (Enghoff 1983: figs 6, 8, 10, 12). [PORTUGAL]: Madeira .... ***A. portosantoensis*** Enghoff, 1983
– Length of metazonital setae of midbody rings > 10% of body vertical diameter. Metazonites smooth 11

11. Flange of posterior gonopod apically tapering, continuous with filamentous tip, basally sometimes evenly rounded, sometimes with more or less well-marked angle (Enghoff 1983: figs 52–54). [PORTUGAL]: Madeira . ... ***A. atlanticus*** Attems, 1937
– Flange of posterior gonopod apically clearly set off vis-à-vis filamentous tip 12

12. Length of metazonital setae of midbody rings 22–33% of body vertical diameter (Enghoff 1983: fig. 15); flange of posterior gonopod large, smooth, rounded, protruding (Enghoff 1983: fig. 63, similar to Fig. 16B in present paper). Subapical emargination of coxal processes obvious (Enghoff 1983: fig. 62) [PORTUGAL]: Madeira .... ***A. serratus*** Enghoff, 1983
– Length of metazonital setae of midbody rings 16–18 % of body vertical diameter; flange of posterior gonopod usually not completely smooth. Subapical emargination of coxal processes shallow or only very slightly indicated 13

13. Subapical emargination of coxal processes only very slightly indicated (Figs 13A, B, 14A). Flange of posterior gonopod massive, apically truncate (Figs 14D–F, 15B). SPAIN: Burgos, Zaragoza (Iberian System) .... ***A. celtibericus*** Gilgado & Enghoff sp. nov.
– Subapical emargination of coxal processes very shallow, but distinct. Flange of posterior gonopod less massive, apically rounded or tapering (Fig. 16A–B, D–E). SPAIN: Ávila, Madrid, Segovia (Central System) .... ***A. continentalis*** Enghoff, 1986

Discussion

Morphology

The genus *Acipes* presents relatively simple gonopods, which provides few characters for species delimitation. Anterior gonopods are quite similar across species, leaving as main characters the relative length/width of the coxal processes, their distal emargination, the shape of their tip, and the relative length of telopodites. Posterior gonopods present more variability across species, with characters such as their relative length/width, the presence or absence of a distal flange with different shapes, serrulated or not, the presence or absence of a filamentous tip of different lengths, serrulated or not, etc. Some species, such as *A. bifilum*, *A. lateralis*, or *A. waldeni* present clearly distinct posterior gonopods; but those of the remaining species are more similar among them. The species *A. alicantinus* sp. nov., *A. andalusius*, *A. celtibericus* sp. nov. *A. continentalis*, *A. oligops* sp. nov., *A. portosantoensis* and *A. serratus* present quite similar posterior gonopods (with a serrulated filamentous tip and a flange) and they are similar, to a lesser extent, to *A. atlanticus* and *A. franzi* and *A. machadoi* (flange or filamentous tip more variable). Based only on posterior gonopod morphology, it is tempting to sketch a species group that includes most of the Iberian species, except *A. bifilum*, and the Macaronesian species *A. serratus*. However, the similarity of posterior gonopods alone is probably not enough evidence for phylogenetic proximity.

Despite the general simplicity and similarity of *Acipes* gonopods, there are several other characters that can be used in combination with them for species delimitation. The most relevant ones are the shape of the first pair of male legs, presence and number of eyes, length of setae, number of rings and body size (Enghoff 1983, 1986; Enghoff & Mauriès 1999; Enghoff & Reboleira 2013). The three here described species share a similar gonopod morphology with the Iberian species *A. continentalis* and *A. andalusius* as explained below.

Acipes celtibericus sp. nov. is most similar to *A. continentalis* (size, colour, number of ommatidia, shape of first pair of legs of male, posterior gonopods with filamentous tip and serrulate flange, accessory claw in midbody legs, etc.), but differs in the shape of the coxal processes of anterior gonopods, and the shape of the flange of posterior gonopods. The gonopods of *Acipes celtibericus* sp. nov. also shows resemblances with the geographically nearest species, *A. oligops*, *A. andalusius* and *A. alicantinus* sp. nov. (serrulate apical margin of flange, filamentous tip), but *A. celtibericus* differs in several other characters such as the first pair of male legs and number of ommatidia. As mentioned above, their gonopods also seem to show more similarities with Macaronesian species, such as *A. serratus*, than with the troglobiont continental Portuguese species.

Acipes oligops sp. nov., is similar to *A. continentalis* and *A. celtibericus* sp. nov. in the general shape of its gonopods (presence of a serrulated filamentous tip and flange), but resembles more *A. continentalis* (flange lanceolate, similar emargination of coxal processes of anterior gonopods). In addition to being clearly distinct from congeneric species in the structure of the first pair of legs, *Acipes oligops* is also notable for its very small number of ommatidia (2 to 3 per side, Fig. 17A.) and its size: it is thinner than all other known adult males of *Acipes*, but has a relatively high number (40) of podous rings: adult males of the smallest Macaronesian species, *A. serratus* Enghoff, 1983, with 40 podous rings thus have a body diameter of 0.45–0.53 mm (Enghoff 1983: fig. 59), whereas the holotype of *A. oligops* only measures 0.36 mm in diameter.

Acipes alicantinus sp. nov. is morphologically very similar to *Acipes andalusius*, but it shows several differences that justify its description as a new species. The first pair of legs of male *Acipes alicantinus* is slenderer (Figs 8F, 10F; Enghoff 1983: fig 61). The shape of the distal part of coxal processes of anterior gonopods is different, with a more acute ending in *Acipes alicantinus* (Fig. 9A, C), while it is blunter in *Acipes andalusius* (Fig. 10A–B). *Acipes alicantinus* has a more lanceolate and narrower flange of the posterior gonopod (Fig. 9B, D), while it is rounder or more truncate in *Acipes andalusius* (Fig. 10C–E). *Acipes alicantinus* also differs in its body size from *Acipes andalusius* (Fig. 7B–C). The two species overlap in their size ranges, but *Acipes alicantinus* is shorter and with fewer body rings than *Acipes andalusius* (see Enghoff & Mauriès 1999; Enghoff & Reboleira 2013) (Fig. 7B–C).

Habitat and distribution

The genus *Acipes* is distributed across Macaronesia and the Iberian Peninsula, but it seems to have a stronger preference for subterranean habitats in the Iberian Peninsula (Enghoff 1983; Enghoff & Mauriès 1999; Enghoff & Reboleira 2013). Troglobiont species are distributed in southern Spain and southern Portugal (*A. andalusius*, *A. bifilum* and *A. machadoi*, cave specialists) (Enghoff & Mauriès 1999; Enghoff & Reboleira 2013) and eastern Spain (*A. alicantinus* sp. nov., MSS). The species from central Spain inhabit the MSS but they seem not to be MSS specialists. However, limited sampling efforts in both subterranean and epigean environments suggest that future discoveries could potentially alter these observed patterns.

In Macaronesia, species are found exclusively in epigean habitats (Enghoff 1983; Kime & Enghoff 2017). Two Macaronesian species are associated with deadwood (Enghoff 1983; Kime & Enghoff 2017), and at least one of the new records of *A. continentalis* was from this microhabitat. This suggests that deadwood could serve as a suitable habitat for *Acipes* species and should be targeted for future samplings.

Central Iberian species (*A. continentalis*, *A. celtibericus* sp. nov., and *A. oligops* sp. nov.) occur in the MSS and, except *Acipes celtibericus*, also in surface habitats. The absence of the latter on the surface might be attributed to the lack of sampling in these habitats (only MSS was sampled in the Iberian System). Its morphology suggests a lifestyle similar to that of *A. continentalis*. The reduced number of ommatidia and the reduced size of *A. oligops* compared to other *Acipes* suggests that this species may be predominantly edaphic or subterranean. The capture of only one individual after several years of sampling in the MSS, and only one additional individual on the surface after four hours of visual searching, indicates that it is a species with a low abundance. Another possibility is that the temporal watercourse (Fig. 2) may not be its primary microhabitat. The species might inhabit the soils surrounding the watercourse, entering it only occasionally. The landscape where *Acipes oligops* was found (slate debris within a limestone landscape, Fig. 2) differs from those where *A. continentalis* and *A. celtibericus* were found (mostly siliceous, quartzitic or granitic terrain in the mountains, Figs 1, 3).

Three southern Iberian species (*A. andalusius*, *A. bifilum*, and *A. machadoi*) are restricted to caves, and they can be classified as troglobionts due to their exclusive presence in hypogean habitats and lack of eyes (Enghoff & Reboleira 2013). *Acipes alicantinus* sp. nov. is also a blind subterranean species, so it can be considered as an MSS specialist troglobiont as well. The difference in size between *A. andalusius* and *A. alicantinus* may be related to the different size of the voids they inhabit (larger in caves, smaller in the MSS).

Conclusions

The new central Iberian species of *Acipes* (*A. celtibericus* sp. nov. and *A. oligops* sp. nov.) are most similar to, and likely more closely related to, the other Central Iberian species, *A. continentalis*. On the other hand, the eastern species *A. alicantinus* sp. nov. is morphologically similar to the southern species *A. andalusius*. However, further genetic analyses are needed to clarify the evolutionary relationships among the species.

The biology and ecology of the species of *Acipes* remain poorly understood (Kime & Enghoff 2017). In Macaronesia, they appear to be primarily associated with soils and epigean habitats. In contrast, southern Iberian species tend to be more subterranean, even troglobiont, while central Iberian species occupy an intermediate ecological niche, being found both on the surface and in the MSS.

The presence, and in some cases high abundance, of four *Acipes* species in the MSS (*Acipes alicantinus* sp. nov., *Acipes celtibericus* sp. nov., *Acipes continentalis*, and *Acipes oligops* sp. nov.) suggest that surveying this habitat is a suitable method to increase our knowledge about *Acipes* and other subterranean or partly subterranean millipedes. Also, deadwood should be a focus of future sampling efforts. Given the incomplete knowledge of the diversity and distribution of *Acipes*, and many other Iberian millipedes, targeted sampling should prioritize the vast areas of the Iberian Peninsula with no millipede records, as highlighted in the maps of Kime & Enghoff (2011, 2017, 2021).

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