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(Diplopoda, Chordeumatida, Opisthocheiridae)
from Spain: taxonomy, phenology,
and postembryonic development

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Living specimens of a *C. dissensionis* Gilgado & Andrés n. sp. male.

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A new *Ceratosphys* Ribaut, 1920 (Diplopoda, Chordeumatida, Opisthocheiridae) from Spain: taxonomy, phenology, and postembryonic development

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ABSTRACT

The genus *Ceratosphys* Ribaut, 1920 (Diplopoda, Chordeumatida) includes 26 species, with 21 recorded in the Iberian Peninsula and the Balearic Islands. This study describes a new species, *Ceratosphys dissensionis* Gilgado & Andrés n. sp., from central Spain. For the first time, information on its postembryonic development and phenology is provided for any Iberian Chordeumatida Pocock, 1894. Specimens were collected in a mixed forest in Somosierra (Madrid, Spain) through monthly sampling of 30 litres of leaf litter over a year, processed using Berlese devices, and preserved in 70% ethanol. A total of 1050 specimens of all stages, except stadium I, were obtained. Morphology was studied with optic and scanning electron microscopy. Adults have 30 segments and undergo eight moults during postembryonic development, reaching adulthood in the ninth stadium. The species is univoltine with a life cycle of about one year, moulting approximately once per month. Adults appear in autumn, and their presence in leaf litter is likely related to environmental conditions.

RÉSUMÉ

Un nouveau *Ceratosphys* Ribaut, 1920 (Diplopoda, Chordeumatida, Opisthocheiridae) d'Espagne : taxonomie, phénologie et développement postembryonnaire.

Le genre *Ceratosphys* Ribaut, 1920 (Diplopoda, Chordeumatida) comprend 26 espèces, dont 21 sont signalées dans la péninsule ibérique et les îles Baléares. Cette étude décrit une nouvelle espèce, *Ceratosphys dissensionis* Gilgado & Andrés n. sp., du centre de l'Espagne. Pour la première fois, des informations sur le développement postembryonnaire et la phénologie sont fournies pour un Chordeumatida Pocock, 1894 ibérique. Les spécimens ont été collectés dans une forêt mixte à Somosierra (Madrid, Espagne) par échantillonnage mensuel de 30 litres de litière pendant un an, récoltés grâce à des Berlese et conservés dans de l'éthanol à 70 %. Un total de 1050 spécimens de tous les stades, à l'exception du stade I, a été obtenu. La morphologie a été étudiée au microscope optique et au microscope électronique à balayage. Les adultes ont 30 segments et subissent huit mues au cours du développement postembryonnaire, atteignant l'âge adulte au neuvième stade. L'espèce est univoltine avec un cycle de vie d'environ un an, muant approximativement une fois par mois. Les adultes apparaissent en automne et leur présence dans la litière est probablement liée aux conditions environnementales.

KEY WORDS

Millipedes,
Iberian Peninsula,
central system,
Madrid,
Europe,
soil fauna,
broadleaf forest,
new species.

MOTS CLÉS

Mille-pattes,
péninsule ibérique,
système central,
Madrid,
Europe,
faune du sol,
forêt de feuillus,
espèce nouvelle.

INTRODUCTION

The order Chordeumatida Pocock, 1894 consists of more than 1100 described species (Brewer *et al.* 2012), with 534 of them listed in the Atlas of European Millipedes (Kime & Enghoff 2021). However, the number of European chordeumatidans continues to increase, as recent studies show (Antić & Mauriès 2022; Šević *et al.* 2022). In the Iberian Peninsula, the chordeumatidan fauna encompasses 79 species (Gilgado *et al.* 2017; Kime & Enghoff 2021; Antić & Mauriès 2022), but it is estimated that the current state of knowledge represents only about 20% of the total number of species, in other words that chordeumatidans remain a poorly studied taxonomic group (Spelda 2015). The genus *Ceratosphys* Ribaut, 1920, consists of 26 species, with 21 of them recorded in the Iberian Peninsula and the Balearic Islands, while the remaining species are distributed in western Europe (Belgium, France, United Kingdom) and North Africa (Morocco) (Kime & Enghoff 2021).

Chordeumatidans are generally lithophilous, with many species showing a preference for low temperatures. Therefore, they are often found in habitats such as high mountains, cold caves and tundra environments (Golovatch & Kime 2009; Spelda 2015). Although there are specialists that inhabit high mountain areas above the tree line, a significant number of species are also found in forested regions (Kime & Enghoff 2021). Despite their affinity for colder habitats, the highest diversity of chordeumatidans has been observed in the southern regions of Europe, particularly in the Iberian, Balkan, and Italian Peninsulas (Kime & Enghoff 2021), where they are mostly active during winter (Spelda 2015).

Many aspects of the biology of most chordeumatidans are still little or fully unknown, but some contributions have been made for certain species, including information about their postembryonic development. Chordeumatidans have teloanamorphic development, meaning that moulting and the addition of new segments stops when they reach the adult stadium, with a fixed number of segments per stadium (Enghoff *et al.* 1993; Minelli 2015; Spelda 2015). The number of segments in adults differs between taxa, but it is typically even, ranging from 26 to 32 (Spelda 2015). Most species of Chordeumatida have 30 segments (including telson) and moult eight times during their development to reach adulthood in the ninth stadium; however, species with 26 and 28 segments reach adulthood after the seventh moult, in the eighth stadium (David 1992; Antić 2017). The changes in morphology of each stadium (e.g. number of segments, legs, ommatidia, etc.) have been studied for a few species, although they are often lacking the first stadia (Tabacaru 1965; Pedroli-Christen 1978; Read 1988; David 1989; Tajovsky 1996; Ćurčić & Makarov 1997; Minelli 2015; Antić 2017). Few works also include the phenology of the species, with the time of occurrence of each stadium (Pedroli-Christen 1978; Read 1988; David 1989; Tajovsky 1996). In general, the time needed to complete development in Chordeumatida is one year, although: 1) species living in high mountains may take two or three years; and 2) there

is also certain intraspecific plasticity, as populations of the same species living at higher altitudes, or those affected by occasional droughts in Mediterranean areas, may take longer (David 1989, 1992; Tajovsky 1996). There are no available data on the postembryonic development and phenology of Iberian Chordeumatida and the only information about the postembryonic development of any species of the genus *Ceratosphys* is the eye development of *Ceratosphys* (?) *amoena* Ribaut, 1920 (Demange 1972; Enghoff *et al.* 1993).

Recent monthly surveys conducted in an oak and birch forest in Somosierra (Madrid, Spain) have resulted in the capture of numerous individuals at different stages of postembryonic development of a previously undescribed chordeumatidan millipede of the genus *Ceratosphys* (family Opisthocheiridae Ribaut, 1913). Here we describe this new species and provide information on its postembryonic development and phenology.

MATERIAL AND METHODS

STUDY AREA

The study area is located in the forest known as ‘Abedular de Somosierra’ (‘Birch Forest of Somosierra’) within the Arroyo de la Dehesa valley, at the western end of the Sierra de Ayllón, in the eastern region of the Puerto de Somosierra pass (Somosierra, Madrid, Spain; 41°07’30”N, 3°34’40”W; 1410 m) (Fig. 1A, B). Map (Fig. 1A) was created using an orthoimage from SIGPAC Viewer (FEGA 2022) overlapping contour lines from a cartographic map downloaded on Instituto Geográfico Nacional (Instituto Geográfico Nacional 2015) using the Photoshop CS7 Portable software.

The geology of the region shows a succession of pelitic-sandy sequences ranging from Ordovician to Lower Devonian, accompanied by gneisses displaying a moderate to low degree of metamorphic alteration (López-Olmedo *et al.* 2020). From a biogeographical point of view, the study area belongs to the Mediterranean region, specifically the Mediterranean-Iberian-Western province, belonging to the Carpetano-Leonesa subprovince, within the Guadarrámico sector, as described by Rivas-Martínez (1987). The ‘birch forest’ is actually a mixed forest consisting mainly of *Betula pendula* ssp. *fontqueri* (Rothm), but also includes several other species such as *Corylus avellana* L., *Ilex aquifolium* L., *Quercus petraea* (Mattuschka) Liebl., *Quercus pyrenaica* Willd and *Pinus sylvestris* L. (Castroviejo 1986–2012; Ferreras & Arocena 1987; Lázaro-Lobo *et al.* 2017) (Fig. 1B).

The study area has an Oceanic Mediterranean climate (Csb) according to the Köppen classification, characterized by mild, wet winters, cool summers and even precipitation throughout the year. However, the Puerto de Somosierra allows northwestern humid winds to enter, leading to cryptoprecipitation in the valley. This results in temperature moderation and increased humidity as compared to neighbouring areas (López-Estébanes & Sáez-Pombo 2002). Data from two weather stations, Buitrago de Lozoya (14.2 km away) and Somosierra (0.7 km away), were used to record daily maximum, minimum, and average temperatures, as well as total precipitation.

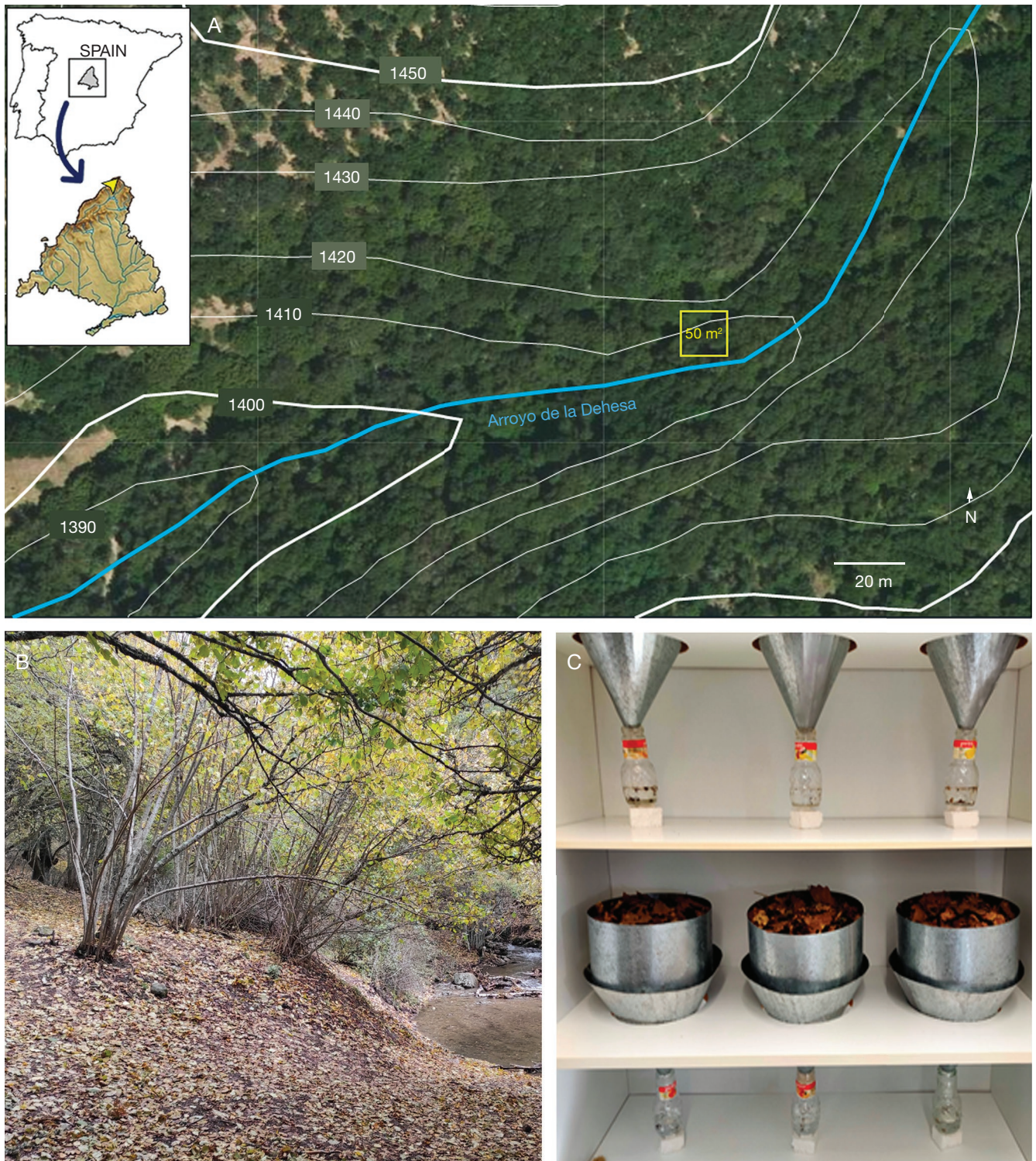


FIG. 1. — Location of sampling sites and sampling methodology: **A**, topographic profile with altitudinal contour lines (white) and map of the study area (type locality of *C. dissensionis* n. sp.); **B**, sampled mixed forest landscape; **C**, Berlese devices with leaf litter and collection jars.

SAMPLING METHODOLOGY

A total of 30 litres of leaf litter per sampling was collected by random sampling in an area of 50 m² on the right bank of the stream, predominantly overgrown with oak leaves

(*Quercus pyrenaica*) (Fig. 1A). The leaf litter was collected once a month for one year (Table 1), from 18.V.2021 to 18.V.2022, transported to the laboratory and dried in Berlese funnels for 10 to 15 days (Fig. 1C). A container

TABLE 1. — Number of segments, legs and ommatidia of the different post-embryonic stadium of *C. dissensionis* n. sp. and the number of specimens collected by sampling, date, and stadium.

Development	Stadium		I	II	III	IV	V	VI	VII		VIII		Adults		Total
									♂	♀	♂	♀	♂	♀	
	Number of rings		7	8	11	15	19	23	26		28		30		
Sampling and date	Spring	M1	18.V.2021	–	23	74	125	10	–	3	13	–	–	–	248
		M2	18.VI.2021	–	–	15	82	237	134	3	–	–	–	–	471
		M3	18.VII.2021	–	–	–	–	1	–	–	–	–	–	–	1
	Summer	M4	8.VIII.2021	–	–	–	–	–	–	–	–	–	–	–	0
		M5	19.IX.2021	–	–	–	–	15	13	3	25	–	–	–	56
		M6	18.X.2021	–	–	1	–	1	34	48	2	45	43	–	174
	Autummm	M7	19.XI.2021	–	–	–	–	2	11	38	–	–	13	15	79
		M8	18.XII.2021	–	–	–	–	–	–	–	–	–	–	–	0
		M9	22.I.2022	–	–	–	–	–	–	–	–	–	–	–	0
	Winter	M10	19.II.2022	–	–	–	–	–	–	–	3	2	6	–	11
		M11	19.III.2022	–	–	–	–	–	–	1	3	2	3	–	9
		M12	18.IV.2022	–	–	–	–	–	–	–	1	–	–	–	1
	Spring	M13	18.V.2022	–	–	–	–	–	–	–	–	–	–	–	0

with 70% ethanol was placed under the funnels to collect the falling fauna. The millipede individuals were sorted, counted, labelled and stored in 70% ethanol. Additional individuals of the new species were found in unsorted vials of hand-caught material collected from dead wood in the same area in 2010.

SPECIMEN STUDY

A Nikon SMZ800 stereomicroscope was used to identify and examine all specimens, including counting the segments of each individual in order to determine their developmental stadium. Adult measurements were performed on 15 individuals of each sex (30 in total) using Image J software (Schneider *et al.* 2012).

Gonopods were dissected and prepared for temporal optical microscopy (OM) slides in glycerol and photographed with a Nikon D5100 digital camera attached to a Leica DM 2500 microscope. Specimens for scanning electron microscopy (SEM) were dehydrated in several baths of absolute ethanol and acetone and coated with gold. SEM photographs were taken in the microscopy service of the Universidad de Alcalá (UAH) with a JEOL JSM-IT500. Type material was stored in the Museo Nacional de Ciencias Naturales, Madrid (MNCN) and the Universidad de Alcalá, Madrid; the rest of the material was also deposited in the UAH. Photographs of live specimens were taken with a Nikon 5100 and a Tamron 90 mm macro lens.

We did not follow the gonopod terminology used in previous *Ceratosphys* descriptions (e.g. Gilgado *et al.* 2015), but that of Antić & Mauriès (2022).

ABBREVIATIONS

MNCN Museo Nacional de Ciencias Naturales, Madrid;
UAH Universidad de Alcalá, Madrid.

RESULTS

REMARK

A total of 1063 millipedes were collected, most of which (1050 individuals) belonged to the new *Ceratosphys* species (Table 1; Fig. 2).

The remaining specimens belonged to species widely distributed in the Iberian Peninsula, such as *Polydesmus coriaceus* Porat, 1871, *Ommatoiulus* cf. *moreleti* (Lucas, 1860) and *Polyxenus lagurus* (Linnaeus, 1758). Along with the millipedes, several ground beetle species were captured and identified (Andrés & Ortuño 2023).

Class DIPLOPODA de Blainville *in* Gervais, 1844
Order CHORDEUMATIDA Pocock, 1894
Family OPISTHOCHERIDAE Ribaut, 1913
Genus *Ceratosphys* Ribaut, 1920

Ceratosphys dissensionis Gilgado & Andrés, n. sp.
(Figs 2-9)

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TYPE MATERIAL. — **Holotype.** Spain • 1 ♂; Madrid, Somosierra, Arroyo de la Dehesa Valley, ‘Abedular de Somosierra’, leaf litter, mixed forest; 41°07’30”N, 3°34’40”W; 1410 m a.s.l.; 18.X.2021; Andrés E. & Ortuño V. M. leg; MNCN 20.07/2148.

Paratypes. Spain • 5 ♂, 5 ♀; Madrid, Somosierra, Arroyo de la Dehesa Valley, ‘Abedular de Somosierra’, leaf litter, mixed forest; 41°07’30”N, 3°34’40”W; 1410 m a.s.l.; 18.X.2021; Andrés E. & Ortuño V. M. leg; MNCN 20.07/2149-2158 • 5 ♂, 5 ♀; same data as for preceding; UAH 95-99.

OTHER MATERIAL STUDIED (SEE ALSO TABLE 1 FOR STADIA). — Spain • 248 juveniles; Madrid, Somosierra, Arroyo de la Dehesa Valley, ‘Abedular de Somosierra’, leaf litter, mixed forest.; 41°07’30”N, 3°34’40”W;



FIG. 2. — Living specimens of a *C. dissensionis* Gilgado & Andrés n. sp. male (A) and female (B) in their habitat.

1410 m a.s.l.; Andrés E. & Ortuño V. M. leg.; 18.X.2021; UAH • 471 juveniles; same data; 18.VI.2021; UAH • 1 juvenile; same data; 18.VII.2021; UAH • 56 juveniles; same data; 19.IX.2021; UAH • 34 ♂, 33 ♀, 86 juveniles; same data; 18.X.2021; UAH • 13 ♂ 15 ♀, 51 juveniles; same data; 19.XI.2021; UAH • 2 ♂, 6 ♀, 3 juveniles; same data; 19.II.2022; UAH • 2 ♂, 3 ♀, 4 juveniles; same data; 19.III.2022; UAH • 1 juvenile, same data; 18.IV.2022;

UAH • 1 ♂, 4 juveniles; same locality in deadwood; 15.X.2010; Gilgado J. D. & Ortuño V. M. leg.; UAH.

ETYMOLOGY. — The authors could not agree on a name for the new species, so after long discussions we decided to ‘agree to disagree’ and dedicate the species name to our ‘disagreement’ (nominative *dissensio*, genitive singular *dissensionis* in Latin).

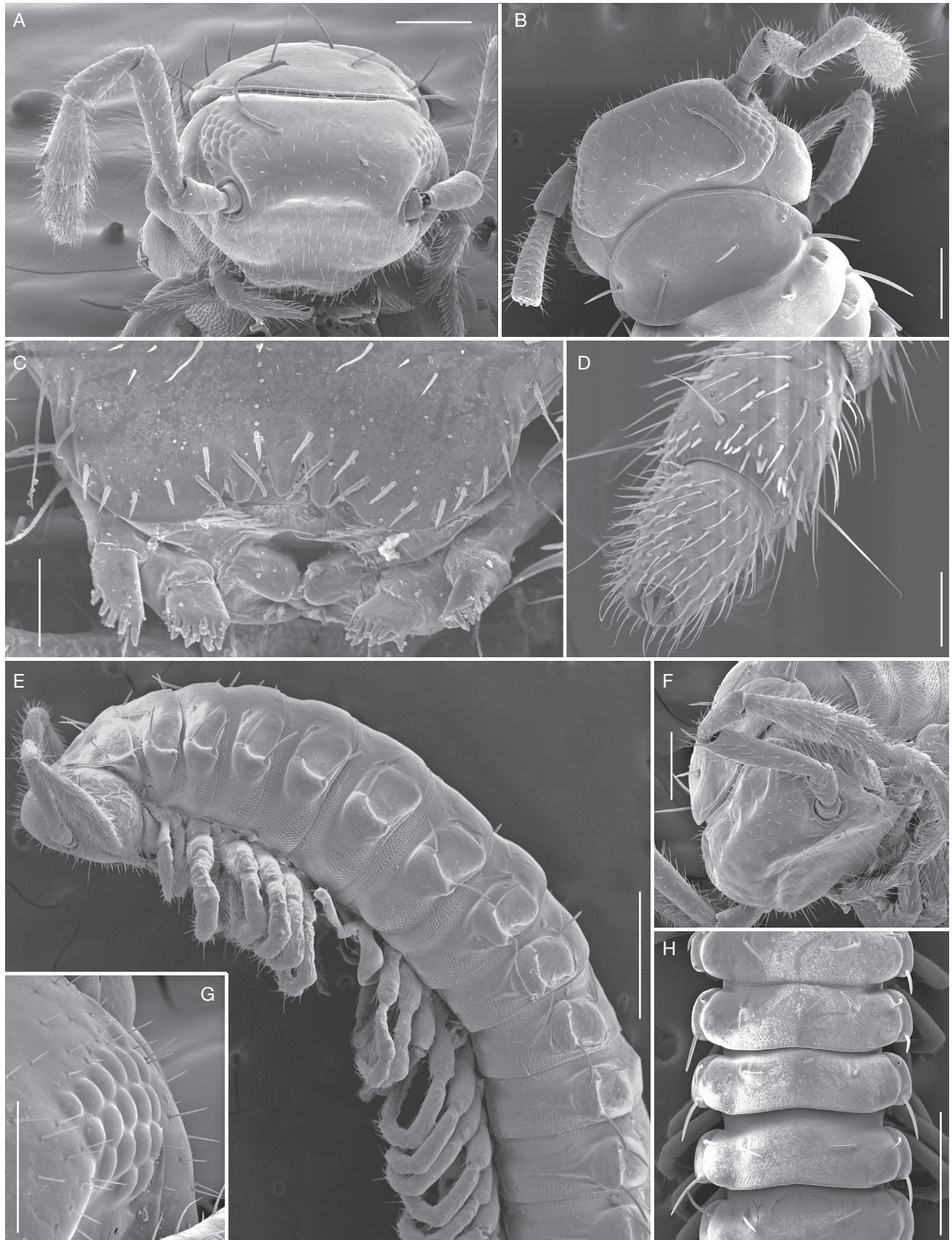


FIG. 3. — Morphology of the head and trunk of an adult male *C. dissensionis* Gilgado & Andrés n. sp. paratype: **A**, head in dorsoanterior view; **B**, head and collum in dorsal view; **C**, labrum in anterior view; **D**, antennomeres VI and VII of right antenna in ventromesal view; **E**, head and first 13 segments in left view; **F**, head in antero lateral left view; **G**, details of the ommatidia of left eye in anterior view; **H**, mid-body segments in dorsal view. Scale bars: A, B, F, 0.2 mm; C, E, H, 0.5 mm; D, 0.05 mm; G, 0.1 mm.

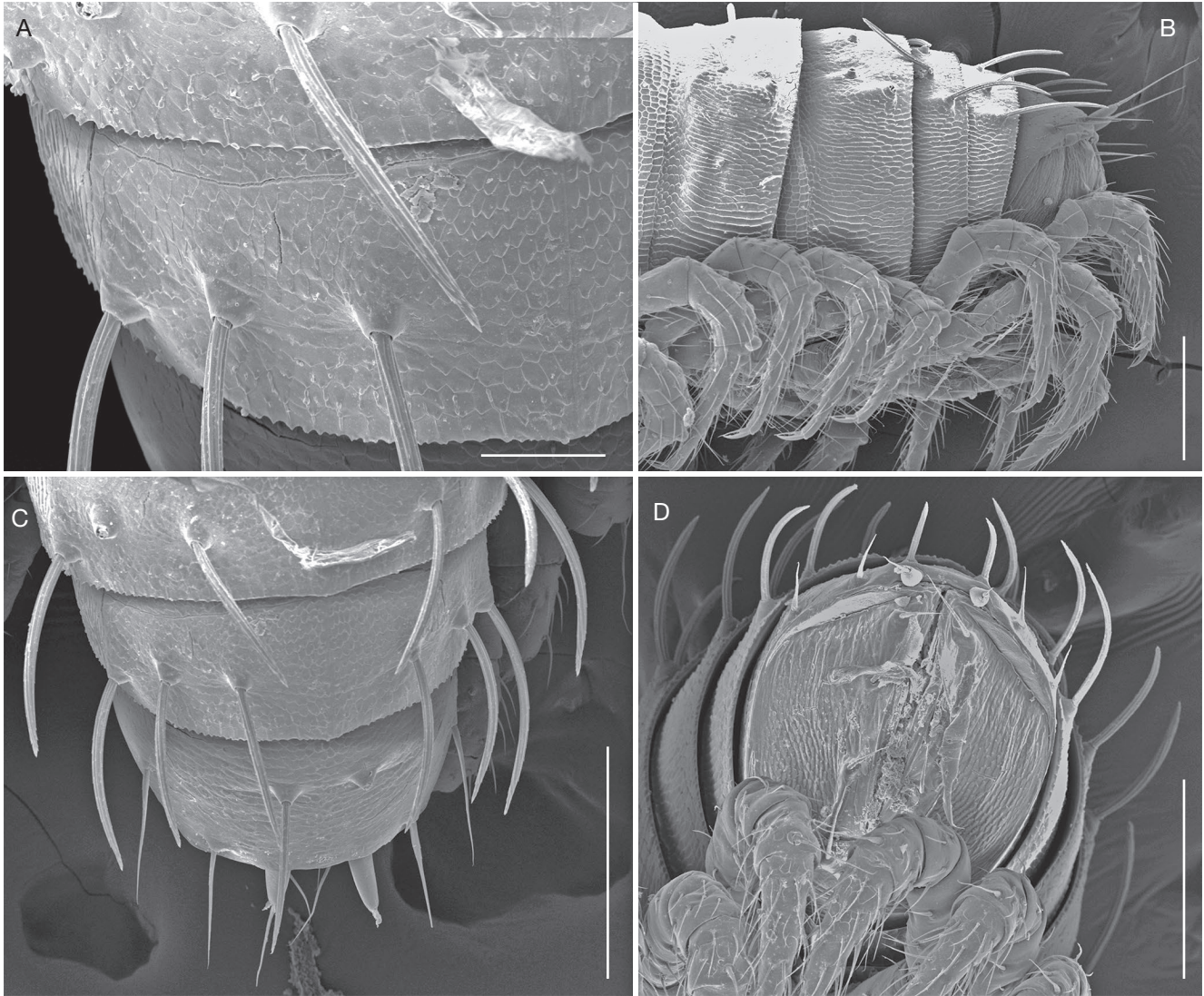


FIG. 4. — The terminal body segments and legs, and telson of an adult male of *C. dissensionis* Gilgado & Andrés n. sp. paratype: **A**, details of the margin of the final segments before the telson in dorsal view; **B**, last body segments and telson in left lateral view; **C**, last segments and telson in dorsal view; **D**, telson and paraprocts (anal valves) in posterior view. Scale bars: A, 0.05 mm; B-D, 0.2 mm.

DIAGNOSIS. — This species can be distinguished from other *Ceratosphys* by the combination of the following characters of anterior gonopods: angiocoxites of anterior gonopods with a single branch and possessing three tips, but lacking brush-like structures, and lyre-like syncolpocoxite, combination not present in any other species of the genus; and posterior gonopods: combination of both a smaller curved colpocoxite (C) and a larger “hook-like”-shaped horn (h) in posterior gonopods, different from the processes in all other *Ceratosphys* species.

DESCRIPTION

Measurements

Adults with 30 segments (including telson). Amber colour, with metazonites darker brownish, basal part of legs light amber with darker distal parts (Fig. 2). Male body size: 8.07–9.23 mm (average 8.71 mm) long, 0.64–0.81 mm (average 0.73 mm) maximum height, and 0.78–1.03 mm (average

0.88 mm) maximum width. Female: 9.66–10.6 mm (average 10.07 mm), 0.83–0.96 mm (average 0.88 mm) and 0.97–1.12 mm (average 1.07 mm), respectively.

Head

No remarkable characteristics, covered with scattered setae, labrum with three teeth, and 8 + 8 setae (6 + 6 labral and 2 + 2 supralabral), but some males showing a higher number of setae (Fig. 3C), frons concave in males (Fig. 3A; F), convex in females (Fig. 8A), with 19–21 ommatidia in males and 19–22 in females, in a triangular field arranged in six vertical rows (*sensu* Enghoff *et al.* 1993); and six rows *sensu* Demange (1972), parallel to the ventral edge of the head capsule, rugose (cobblestone paving-like) area posterior to insertion of antennae. Antennomeres I–VII measuring: 0.06, 0.13, 0.36, 0.20, 0.29, 0.11 and 0.07 mm from base

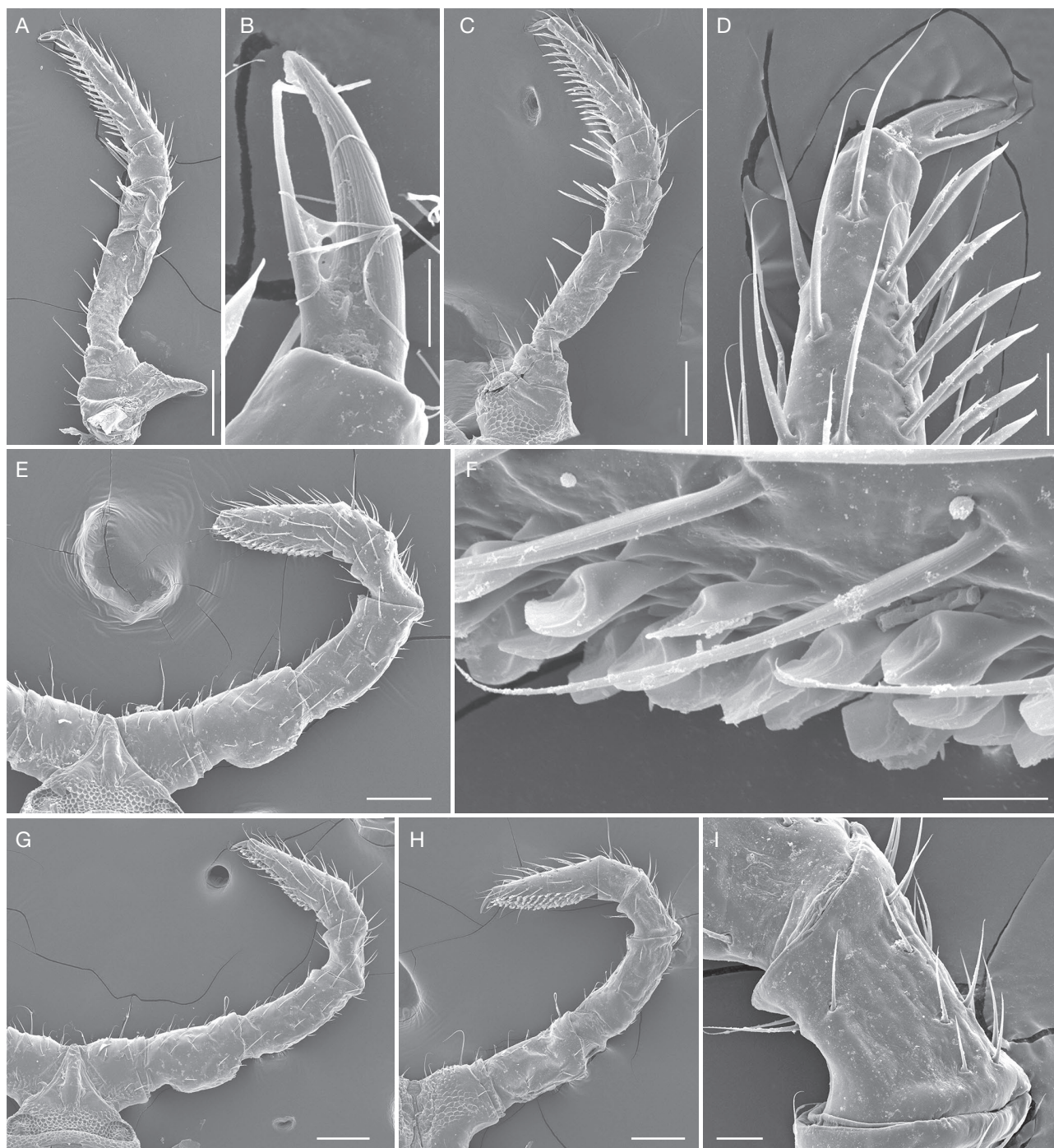


FIG. 5. — Legs 1-5 of an adult male of *C. dissensionis* Gilgado & Andrés n. sp. paratype: **A**, leg 1; **B**, details of the claw and accessory claw of leg 1; **C**, leg 2; **D**, details of the tip of leg 2; **E**, leg 3; **F**, details of the modified setae of leg 3, **G**, leg 4, **H**, leg 5; **I**, detail of the postfemur of leg 5. Scale bars: A, C, E, G, H, 0.1 mm; B, F, 0.01 mm; D, I, 0.02 mm.

to apex in male holotype, respectively, and with numerous setae, especially on the seventh antennomere surface. Basiconic sensillae present ventrodistally in distal antennomeres (Figs 3D; 8A).

Trunk

Collum with 3 + 3 setae, 1 + 1 paramedian, 2 + 2 lateral (Fig. 3B). Following segments with same chaetotaxy. Paranota increasing

in size up to the seventh segment, maintaining approximately the same size in the next six segments, and then decreasing in size until fading towards the last segments of the body in both sexes (Fig. 2; 3E, H; 4). Prozonites and ventrolateral parts of metazonites with a cell- or scale-like microsculpture, dorsal part of metazonites and paranota relatively smooth (Figs 3C; 4A, B). Posterior margin of last segments almost serrulate (Fig. 4A).

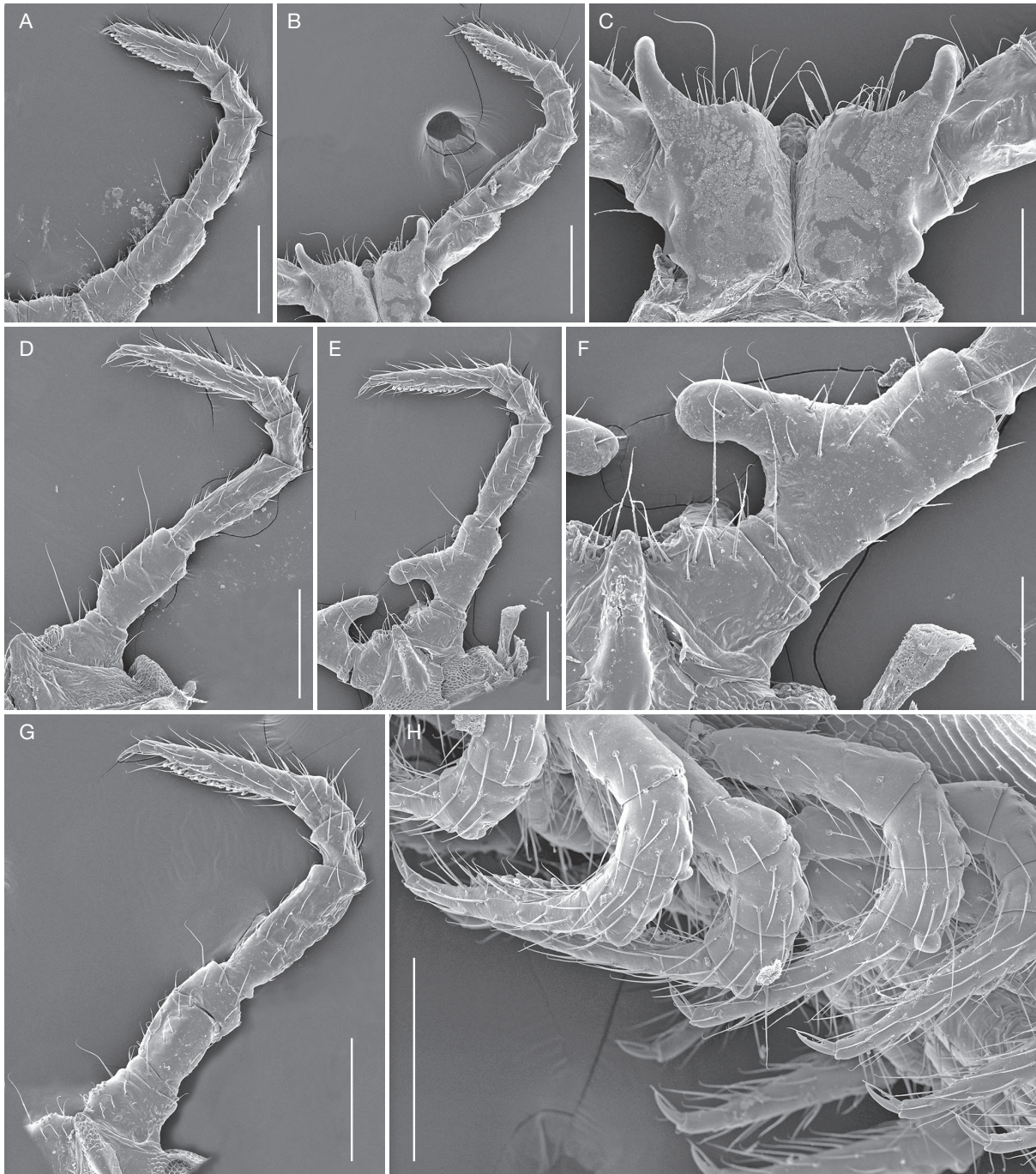


FIG. 6. — Legs 6–7, 10–12, and 43–49 of an adult male *C. dissensionis* Gilgado & Andrés n. sp. paratype: **A**, leg 6; **B**, leg 7; **C**, details of the coxae of leg pair 7; **D**, leg 10; **E**, leg 11; **F**, details of the prefemur of leg 11; **G**, leg 12; **H**, legs 43–49 in the posterior part of the body; segments 24–27, in lateral view. Scale bars: A, B, D, E, G, H, 0.2 mm; C, F, 0.1 mm.

Legs

Leg pairs 1 and 2 smaller in both sexes, with tarsal combs; femora, postfemora and tibiae with long and robust setae ventrally (Fig. 5A–D). Leg pairs 3–7 incrassate in males. Leg pairs 3 and 4 with dorsal, rounded bulge on prefemur, a dorsally depressed, slightly concave postfemur (Fig. 5E–G). Leg pair 5 similar but without a rounded bulge on prefemur, while postfemur is straight rather than concave (Fig. 5H, I). Leg pair 6 similar, with a concave postfemur (Fig. 6A). Leg pair 7 with

modified coxae, mesally rugose, laterodorsally with a small, rounded protrusion, lateroventrally with a conical curved protrusion with a blunt tip half as long as the prefemur. Prefemur with a central concavity where these conical protrusions presumably fit (Fig. 6B, C). Leg pair 10 slender, with coxal sacs, and prefemora showing a subtle conical ventrad protrusion (Fig. 6D). Leg pair 11 with coxal sacs, and prefemora with a mesad ‘big toe-like’ process with a blunt rounded tip (Fig. 6E, F). Leg pairs 12 onward without remarkable characters



Fig. 7. — Gonopod morphology of a *C. dissensionis* Gilgado & Andrés n. sp. paratype: **A**, left lateral view of body with legs and the distal part of gonopods visible; **B**, posterior view of the anterior and posterior gonopods; **C**, posterior view of the anterior gonopods; **D**, posterior view of anterior gonopods; **E**, lateral view of the left angiocoxite of anterior gonopod; **F**, lateral view of left angiocoxite of anterior gonopod; **G**, anterior view of anterior gonopods; **H**, anterior view of syncolpocoxite of anterior gonopods; **I**, anterior view of right posterior gonopod; **J**, posterior view of the posterior gonopod, **arrow** points at vestiges of articulations; **K**, posterior view of the posterior gonopod, **arrows** point at vestiges of articulations. Labels: **A**, angiocoxites; **C**, colpocoxite of posterior gonopod; **cA**, concave space of angiocoxite; **cC**, column of Syncolpocoxite; **Ct**, telopodite of the posterior gonopod; **Cx**, coxite of posterior gonopods; **dA**, distal pointy tip of the angiocoxite; **dC**, depressions of the syncolpocoxite; **h**, horn of the posterior gonopod; **hC**, hole of the syncolpocoxite; **S**, sternum of the posterior gonopods; **SC**, syncolpocoxite; **vA**, ventroanterior pointy foliar process of the angiocoxite; **pA**, posterior pointy tip of the angiocoxite; **w**, widening of the second horn of the posterior gonopod. Scale bars: A, B, G, J-I, 0.2 mm; C-F, H, 0.1 mm.

(Fig. 6G, H). All legs with ventral accessory claw longer than the claw itself (Fig. 5B, D). Tarsal papillae present in all male's legs except the last eight pairs (Figs 5E-H; 6A, B, D, E, G, H).

Telson

Epiproct with 3 + 3 setae and 1 + 1 spinnerets (Figs 3C, D). Paraprocts with scale-like microsculpture, and 3 mesal setae each (Fig. 3D). Hypoproct with 1 + 1 setae.

Gonopods (Fig. 7)

Anterior gonopods relatively simple (Fig. 7C-G). Sternum (S) reduced to joining of angiocoxites in their basal mesal part (Fig. 7G) angiocoxites (A) straight, with a distal part curved posteriad. At the middle of angiocoxite, an apparent lateral 'folding' showing a suture (fA). Distal part of angiocoxite with a sharp tip resembling an upper seagull beak (dA). Ventroanteriorly to distal tip, a second tip (vA), formed by a foliar triangular process. Posteriorly to the distal tip, a third tip (pA), leaving a concave space (maybe an opening) (cA) between it and the distal tip. Syncolpocoxite (SC) with "lyre-like" shape, with convex rounded lateral margins, distally ending in two triangular ventrolaterad rugose tips (tC), separated by a suture. In posterior view, 1 + 1 rugose flat depressions (dC) covering a large area of syncolpocoxite, separated by a column (cC) in the middle, and proximally to this column, a smaller hole (hC) (Fig. 7C). In anterior view, with two lateral and longitudinal depressions (lC) to accommodate angiocoxites from its basis to the rugose tips.

Posterior gonopods larger than anterior gonopods, with articulations and vestigial articulations visible (Fig. 7I-K). Gonopodal sternum (S) reduced to a membrane. Telopodites (Ct), with a long distal part and two basal processes: 1) a smaller proximal, mesal, curved and anterolaterad pointing horn, most likely a colpocoxite (C) (or also possibly an angiocoxite), coming out of the coxite (Cx); and 2) a larger lateral, 'hook-like' curved, flattened, mesoposteriad horn ending in a blunt finger-like tip (h). Posterior margin of this second horn widened in its basal half (w). Distal part of telopodite narrow and long and with several setae, with tip pointing laterodorsad. Distalmost part with pigment remnants (pr) and ending in a small presumably membranous process (mt) at the tip.

Vulvae (Fig. 8B, C)

Slightly longer than wide. Operculum (O) with three setae in mesal lobe and five in lateral lobe. Supra-opercular prolongation (sop) of small size. Bursa (B) with a distal concavity in each valve, six setae in mesal and six in lateral lobe. Apodematic groove surrounded by a lateral and mesal lip-like rugose structures, mesal one with small denticles basally. Postvulvar organ (pv) small, curved and with serrated margin. Sternum posterior to vulvae (S) with two depressions (dS) (Fig. 8A, B), and a central knob (kS) reaching coxae of leg pair three.

POSTEMBRYONIC DEVELOPMENT

The number of segments, legs and ommatidia increases with the growth of the individuals as shown in Table 1. Morpho-

logical differences were observed between all stadia examined (Table 1; Fig. 9) except stadium I. The length of *C. dissensionis* Gilgado & Andrés, n. sp. increases 10 times from approximately 1 mm (stadium II) to 10 mm (adult females). The number of segments increases by three between stadia II-III and between stadia VI-VII; by four segments at each moult between stadia III to VI; and by only two segments at the moults between stadium VII and the adult stage. The number of legs increases according to two leg pairs per segment, except for the differences observed in males due to the presence of anterior and posterior gonopods. Thus, females have 49 pairs of legs, while males have 47 pairs of legs. The number of ommatidia also increases non-linearly with each moult (Table 1).

PHENOLOGY

Both the activity of *C. dissensionis* Gilgado & Andrés, n. sp. and the climatic conditions (temperature and precipitation) showed monthly fluctuations during the one-year sampling period, between 18.V.2021 and 18.V.2022. The climatogram (Fig. 10) shows that the highest average temperature (21.7°C) was measured in the summer months and the lowest (4.6°C) at the end of winter. The heaviest precipitation fell between April and May 2022, while there was a minimal amount of precipitation between August and November 2021. However, a certain consistency of precipitation was observed in the study area during the sampling period. The presence of *C. dissensionis* Gilgado & Andrés, n. sp. in the leaf litter was recorded throughout the year, except during the sampling in August and December 2021 and in January and May 2022 (Table 1; Fig. 10). Adults of this species have been observed at two different periods of the year: most specimens (58 males and 56 females) were collected at the beginning of autumn, while a few individuals (four males and nine females) were collected during late winter sampling. No specimens of stadium I have been found in the field, and all stadium II samples (23 specimens) were found in May of the first year. The majority of the stadium III individuals were collected in May and June, with only one specimen found in October. This pattern appears to coincide with the highest proportion of adults recorded in autumn and the smallest proportion of adults in spring, indicating a developmental delay in part of the *C. dissensionis* Gilgado & Andrés, n. sp. population. We did not record any mating couples of this new species in the study area.

DISCUSSION

MORPHOLOGY

The general morphology of the gonopods is consistent with the general shape of the genus *Ceratosphys*, but there is a large variation among species. There seem to be a clear homology between the most conspicuous structures of anterior gonopods (colpocoxites and angiocoxites) across the genus. These structures seem to have a coxal origin, as in most chordeumatids (Antić & Mauriès 2022). However, some structures are only present in some species, such as the brush-like structure or anterior horns in *C. amoena*, *Ceratosphys deharvengi* Mauriès,

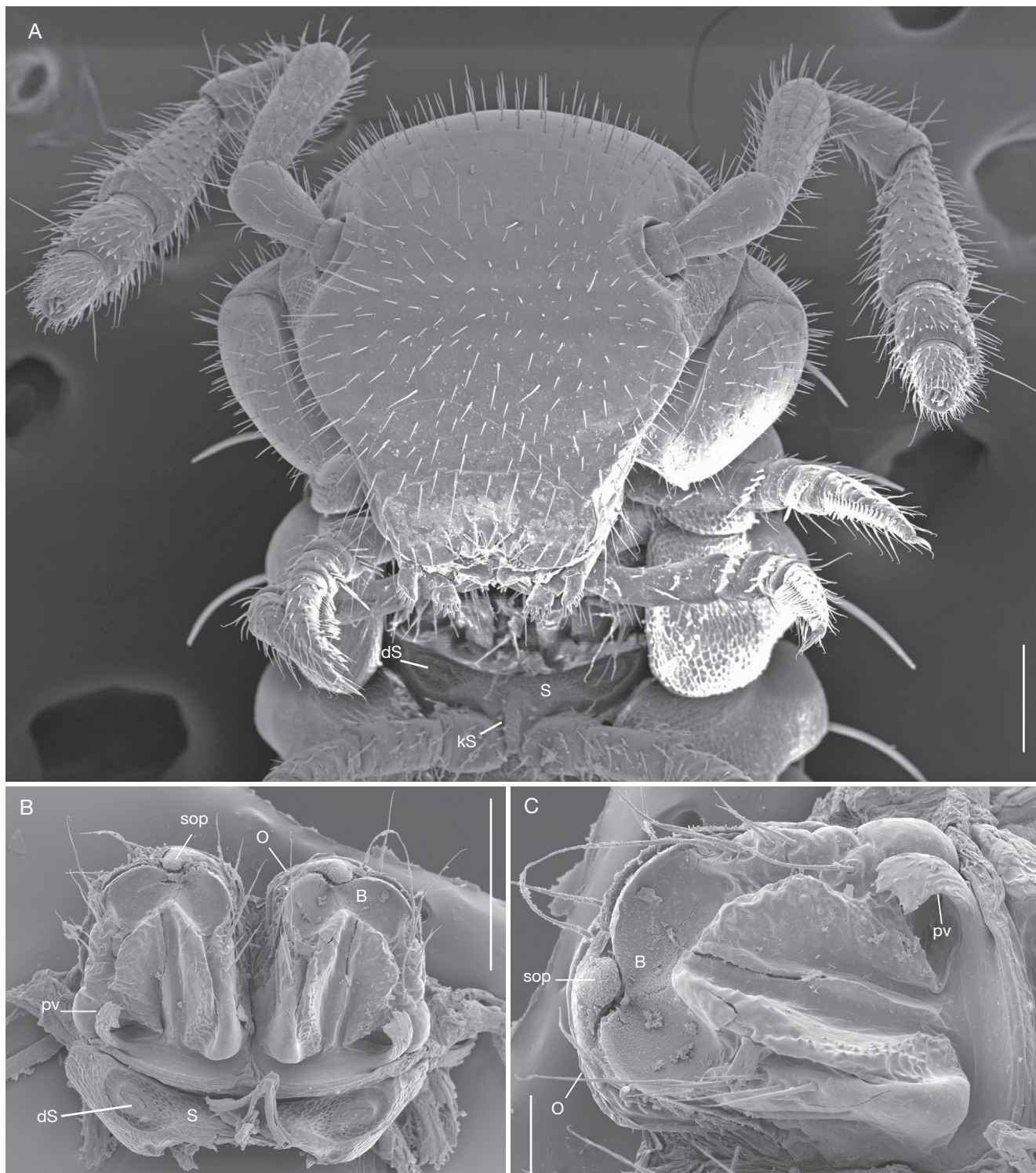


FIG. 8. — Details of a female specimen of *C. dissensionis* Gilgado & Andrés n. sp. paratype: **A**, head in frontal view and first rings in ventral view; **B**, dissected vulvae in ventroposterior view; **C**, left vulva in posteroventral view. Labels: **B**, bursa; **ds**, depressions of Sternum; **ks**, knob of sternum; **O**, operculum; **pv**, post-vulvar organ; **S**, sternum; **sop**, supra-opercular prolongation. Scale bars: A, B, 0.2 mm, C, 0.05 mm.

1978 or *Ceratosphys taurus* Ribaut, 1956, absent in *C. dissensionis* Gilgado & Andrés, n. sp. There is also a strong variation in size and shape of posterior gonopods. Some species have quite reduced and simple posterior gonopods, such as *C. amoena*, *Ceratosphys geronensis* Mauriès, 1963, *Ceratosphys hispanica*

Ribaut, 1920, *Ceratosphys simoni* Ribaut, 1920, *C. taurus* or *Ceratosphys vandeli* Mauriès, 1963. Some other species have posterior gonopods with longer telopodites, with or without processes of different sizes, such as *Ceratosphys angelieri* Mauriès, 1964, *Ceratosphys bakeri* Mauriès, 1990, *Ceratosphys*

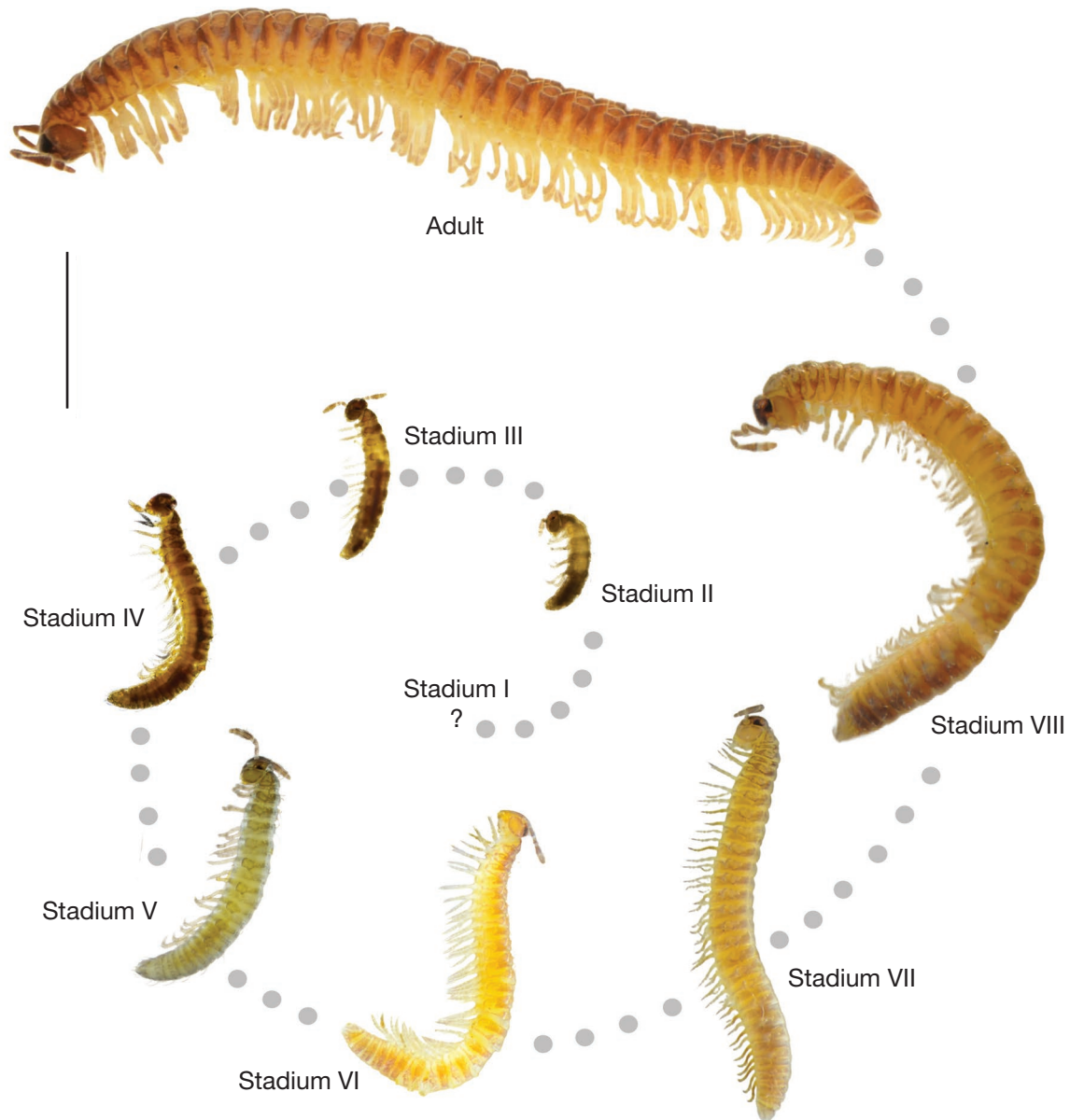


FIG. 9. — Postembryonic development of *C. dissensionis* Gilgado & Andrés n. sp. from stadium II to adult. Scale bar: 2 mm.

fernandoi Mauriès, 2014, *Ceratosphys guttata* Ribaut, 1956, *Ceratosphys jabaliensis* Mauriès, 2013, *Ceratosphys poculifer* (Brölemann, 1920) or *Ceratosphys vicentae* Mauriès, 1990.

The shape of the angiocoxites of anterior gonopods of *C. dissensionis* Gilgado & Andrés, n. sp. (Fig. 7C-F) are somewhat similar to those of *C. amoena*, a species presumably native to the French Pyrenees that can also be found in Belgium and Wales (Kime & Enghoff 2021). However, anterior gonopods of *C. dissensionis* Gilgado & Andrés, n. sp. lack the brush-like structure and the anterior horns (Fig. 7G). The shape and simplicity of angiocoxites of *C. dissensionis* Gilgado & Andrés, n. sp. is also somewhat similar to that of *C. geronensis*, a species from northeastern Spain (Kime & Enghoff 2021), but this species also has a small brush-like structure distally in the angiocoxites. The general shape of anterior gonopods of *C. dissensionis* Gil-

gado & Andrés, n. sp. mostly resembles those of *C. angelieri*, a species from southern Portugal (Kime & Enghoff 2021).

The posterior gonopods of *C. dissensionis* Gilgado & Andrés, n. sp. (Fig. 7I-K) have an articulated telopodite of large size, and two processes proportionally larger than any other process in posterior gonopods of any *Ceratosphys* species. The most basal and smaller process is here interpreted as colpocoxite (Fig. 7J, K), this is, derived from chitinized coxal glands (Antić & Mauriès 2022), but it could also be an angiocoxite, this is, just a process of coxal origin. Other *Ceratosphys* seem to have processes of coxal origin, but their degree of chitinization and origin are difficult to assess without examining specimens, such as *C. angelieri* or *Ceratosphys maroccana* Mauriès, 1985. The large second process (h) of posterior gonopods of *C. dissensionis* Gilgado & Andrés, n. sp. seems to be of prefemoral

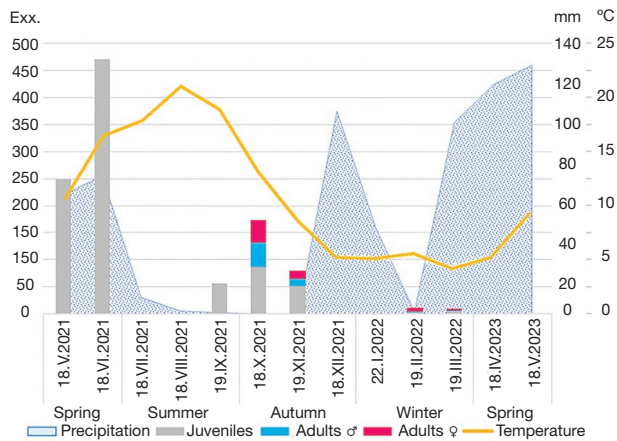


FIG. 10. — Climograph with average temperature (yellow line) and accumulated precipitation (blue polygon) on each sampling date. Bar chart with number of total specimens differentiated by juveniles (grey), males (blue) and females (pink) per sampling.

origin, as a vestigial articulation can be observed between the process and the coxite (Fig. 7J, K). Other *Ceratosphys* species have processes of different sizes that are clearly of prefemoral origin, such as *C. guttata*, *C. jabaliensis*, *Ceratosphys nivium* Ribaut, 1927. Two *Ceratosphys* species have large prefemoral processes in the posterior gonopods, almost of similar proportional size to those of *C. dissensionis* Gilgado & Andrés, n. sp. This is the case of *C. poculifer*, a species also from Central Spain but living at lower elevation, and *C. vicenteae*, from western Spain. The posterior gonopods of *C. vicenteae* seem to be the most similar to those of *C. dissensionis* Gilgado & Andrés, n. sp. The drawings in Mauriès (1990) show that posterior gonopods of *C. vicenteae* have a process of coxal and one of prefemoral origin touching each other. The exact mechanical role played by the large processes of posterior gonopods remains unknown.

The vulvae of genus *Ceratosphys* show two characters which are also present in *C. dissensionis* Gilgado & Andrés, n. sp.: a supra-opercular prolongation, and a postvulvar organ (Fig. 8B, C). These two structures have different sizes and shapes among species, and in some cases they are absent. The supra-opercular prolongation is large in *C. deharvengi*, *C. jabaliensis*, *Ceratosphys nodipes* (Attems, 1952), *Ceratosphys picta*, Ribaut, 1951, *Ceratosphys solanasi* (Mauriès & Vicente, 1978) and *Ceratosphys toniserra* Mauriès, 2012, but it is small in *C. fernandoi* and *Ceratosphys mariacristinae* Mauriès, 2013, and it seems to be absent in *C. amoena*, *C. angelieri*, and *C. nivium*. In *C. dissensionis* Gilgado & Andrés, n. sp. the supra-opercular prolongation is reduced to a small protuberance (Fig. 8B, C). The postvulvar organ is very long in *C. nivium*, reaching around twice the length of the vulva. It is also relatively long in *C. angelieri*, *Ceratosphys cryodeserti* Gilgado, Mauriès & Enghoff, 2015, *C. deharvengi*, *C. hispanica*, *C. mariacristinae*, *C. picta*, *C. solanasi* and *C. toniserra*. This organ is shorter in *C. amoena*, *C. fernandoi*, *C. jabaliensis*, *C. nodipes*, *C. poculifer* and *C. vicenteae*. The postvulvar organ in *C. dissensionis* Gilgado & Andrés, n. sp. is small, and somewhat similar in shape to that of *C. vicenteae*, *C. nodipes*, and *C. jabaliensis*, although

in the latter it seems to be in a more mesal position, while it is more lateral in *C. dissensionis* Gilgado & Andrés, n. sp.

HABITAT AND DISTRIBUTION

The genus *Ceratosphys* is not consistent in its habitat preference, with some species inhabiting caves, stony areas, forests, bushes, shrubs, mountains, or lowlands (Kime & Enghoff 2021). There is no detailed information about the habitat of the most similar *Ceratosphys* species according to gonopod morphology (not necessarily the closest relatives). *Ceratosphys angelieri* was found in the Serra de Monchique, in southern Portugal (300–900 m). *Ceratosphys poculifer* inhabits drier regions with scarcer vegetation in Central Spain at around 700 m (Brolemann 1920), but it has been introduced in the Canary Islands, where it can be found up to 1850 m (Vicente & Enghoff 1999). *Ceratosphys vicenteae* was found in western Spain, in Zamora province, and far from the Central System mountain range. This species was captured at 700 m, but no further habitat information is provided in the original description (Mauriès 1990). *Ceratosphys dissensionis* Gilgado & Andrés, n. sp. has only been found in a mixed forest with oaks and birches, but no similar sampling was carried out in other habitats such as the bushy areas or the coniferous forests that are abundant in the surrounding areas. There is not enough evidence to determine whether *C. dissensionis* Gilgado & Andrés, n. sp. feeds on a specific tree species in the mixed forest (birch, oak, etc.) or whether it may be a more generalist species feeding on different broadleaf species. This may influence its actual range, as birch trees are rare in central Iberian Peninsula, appearing mostly in mountain areas, and are virtually absent in the southern half of the peninsula (Blanco *et al.* 2005), while *Quercus pyrenaica* has a wider distribution in these regions. However, *C. dissensionis* Gilgado & Andrés, n.sp. has not appeared in the Mesovoid Shallow Substratum (MSS) in higher elevations in the Sierra de Guadarrama mountain range so far (Ortuño *et al.* 2022), where *Guadarramasoma ramosae* Gilgado, Ledesma, Enghoff & Mauriès, 2017 was captured (Gilgado *et al.* 2017). Therefore, until more sampling is done in the region, we can presume that *C. dissensionis* Gilgado & Andrés, n. sp. is a broadleaf forest inhabitant.

DEVELOPMENT

The number of body segments and pairs of legs in the different stadia of *C. dissensionis* Gilgado & Andrés, n. sp. (Table 1) corresponds to the typical pattern observed in the order Chordeumatida (Enghoff *et al.* 1993) and is consistent with data reported for other species (Antić 2017). In our sampling, the abundance of captured specimens varied among juvenile stadia, with stadia IV and V being the most abundant. The absence of captured individuals of stadium I seems to be common in other diplopods according to the observations of other authors (Tabacaru 1963; Pedrolí-Christen 1978; Read 1988; Enghoff *et al.* 1993; Tajovsky 1996; Antić 2017), possibly due to the low mobility of this stadium and the sampling methods used.

According to our data, the development of *C. dissensionis* Gilgado & Andrés, n. sp. occurs at a rate of approximately one moult per month, between April and November, and sexual development is completed in autumn.

PHENOLOGY

Several researchers (e.g. David 1989, 1992; Meyer 1990; Tajovsky 1996) have found that the developmental process in chordeumatidan species takes usually one year, a pattern that appears to align with observations in *C. dissensionis* Gilgado & Andrés, n. sp. However, these authors have observed a strong dependence of the biological cycle of chordeumatidans on environmental conditions, particularly humidity. It has been documented that the life cycle of certain chordeumatidan species living in arid Mediterranean climates or in high mountains can extend up to three years (Meyer 1990; David 1992). For instance, David (1989) documented that a drought in 1985 had a significant impact on the population of the species *Chamaesoma brolemanni* Ribaut & Verhoeff, 1913, and Tajovsky (1996) also noted a decline in the population density of *Melogona voigtii* (Verhoeff, 1899) during a drought period. However, the absence of *C. dissensionis* Gilgado & Andrés, n. sp. individuals in our samples during the cold months of December and January does not correspond to an absence of precipitation in the study area (Fig. 10). However, it could also be related to a decrease in temperature, which indicates a multi-layered influence on their seasonal occurrence. No specimens were found in July and August either (only one specimen). This could be due to the temperature (in this case an increase), perhaps in conjunction with the lack of summer rainfall. As our sampling method was to bring leaf litter into the laboratory, the absence of individuals does not necessarily reflect just a lack of activity, but rather a genuine absence of individuals in the leaf litter. This suggests that these millipedes are likely to seek shelter in other microhabitats (e.g. underground) during these times of harsh conditions.

The annual biological cycle of *C. dissensionis* Gilgado & Andrés, n. sp. exhibited the highest number of adults in October and November, which coincides with observations made by Read (1988), David (1989) and Tajovsky (1996) in other chordeumatidans such as *Chordeuma proximum* Ribaut, 1913, *C. brolemanni* and *M. voigtii* respectively. The presence of adults in these months, along with the appearance of stadium II in May, suggests the possibility of mating and oviposition taking place between November and April. This observation agrees with the results of Read (1988) and Tajovsky (1996), who discovered eggs in the ovaries of *C. proximum* and *M. voigtii* females during these same months. On the other hand, Pedroli-Christen (1978) and Tajovsky (1996) also suggested that part of the population might enter a state of hibernation during stadia VI and VII when microclimatic conditions are unfavourable. In our case, this would correspond to the absence of individuals in our samples during the summer months and could be due to the high temperatures, lower precipitation, or both (Fig. 10). This delayed development may explain the presence of a group of adults of *C. dissensionis* Gilgado & Andrés, n. sp. (and specimens of stadia VI and VII) during the end of the winter. We have not been able to explain the absence of specimens in May of the second year, in contrast to the almost 250 specimens collected in May of the first year, considering that temperature conditions were similar, and rainfall was recorded in both samples.

CONCLUSIONS

The discovery of *Ceratosphys dissensionis* Gilgado & Andrés, n. sp. is a small step in the progress of the study of the unknown Iberian Chordeumatida. The morphology of the posterior gonopods of *C. dissensionis* Gilgado & Andrés, n. sp. clearly distinguish it from its most similar relatives. Regarding its life cycle, *C. dissensionis* Gilgado & Andrés, n. sp. seems to be univoltine, with most adults appearing in autumn, around October. However, some adult specimens can also be found until March, most likely because some individuals take longer to develop, as suggested by the presence of individuals of stadia VI, VII or VIII during October, November, and February. However, *C. dissensionis* Gilgado & Andrés, n. sp. could not be found throughout the entire year, and during two periods of the year, the species was virtually absent in the leaf litter. This occurred during the coldest months of the year (December and January) and the hottest months (July and August) (Fig. 10). Absence during winter was not related to a lack of humidity, but presumably due to low temperature, while absence during summer could be explained by the high temperatures and/or lower humidity and precipitation. The postembryonic development of *C. dissensionis* Gilgado & Andrés, n. sp., that is, the number of segments added in each moult, agrees with that of other chordeumatidans.

Ceratosphys dissensionis Gilgado & Andrés, n. sp. has only been found in leaf litter mainly composed of *Quercus* and *Betula* leaves, in a well-preserved, broadleaf humid forest with minimal environmental fluctuations, inhabited by mesophilous, hygrophilous and sciophilous edaphic species (Andrés & Ortuño 2023). Further surveys are needed to clarify the distribution range of the species, its habitat use and its feeding preferences in order to assess its conservation status.

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