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NEW *ORCHESTINA* SIMON, 1882 (ARANEAE: OONOPIDAE) FROM CRETACEOUS AMBERS OF SPAIN AND FRANCE: FIRST SPIDERS DESCRIBED USING PHASE-CONTRAST X-RAY SYNCHROTRON MICROTOMOGRAPHY

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Abstract: Two new species of *Orchestina* (Araneae: Oonopidae) are described as *O. gappi* sp. nov. and *O. rabagensis* sp. nov. from the Cretaceous of France and Spain, respectively. Two additional specimens from Spain are placed within *Orchestina* but not assigned to species. These formal descriptions are the oldest for the genus and the family Oonopidae. The discovery of these older *Orchestina* is not surprising, as the genus is considered a basal member of the Oonopidae and one of the most diverse and long-lived spider lineages. Two of the spiders were imaged at the European Synchrotron Radiation Facility using propagation phase-contrast X-ray synchrotron microtomography, demonstrating once again the enormous potential of this technique for studying fossil inclusions in amber.

Key words: Arachnida, goblin spiders, amber, Archingeay-Les Nouillers, El Soplao, San Just, Peñacerrada I.

OONOPIDAE Simon, 1890 are small, ecribellate, haplogyne spiders with six eyes and two claws on a pronounced onychium (Jocqué and Dippenaar-Schoeman 2006). The family is relatively diverse, with more than 684 extant species in 82 genera. Of the haplogyne families, only the Pholcidae encompasses more species (1122; Platnick 2011). Oonopids are free-living, nocturnal hunters and are distributed throughout the world, primarily in the tropics and subtropics. They live in a variety of habitats, such as under bark and stones, in leaf litter, among foliage and in the webs of other spiders (Saaristo 2001; PBI 2010).

Oonopids belong in the superfamily Dysderoidea, containing the Dysderidae Koch, 1837, Segestriidae Simon, 1893*a*, Oonopidae, and Orsolobidae Cooke, 1965 (Forster and Platnick 1985; Platnick *et al.* 1991). Within the Dysderoidea, the family is most closely related to the Orsolobidae based on the shared presence of tarsal proprioreceptor bristles and bipectinate tarsal claws (Forster and Platnick 1985; Platnick *et al.* 1991).

The oonopid fossil record is fairly extensive, comprising over three per cent of described fossil spider species (Dunlop *et al.* 2011). Oonopids have been found in more amber deposits than any other spider family (Penney 2007; Dunlop *et al.* 2011), although they are absent from the sedimentary rock record (probably as a result of their small size, see Martínez-Delclòs *et al.* 2004; Selden and Penney 2010; Penney and Selden 2011). The oldest oonopid was reported from Lebanese amber (late Barremian–early Aptian; Penney 2000) but, hitherto, Cretaceous oonopids have only been described from Burmese (late Albian; Penney 2000, 2006*a*; Rasnitsyn and Ross 2000; Grimaldi *et al.* 2002; Wunderlich 2008), New Jersey (Turonian; Penney 2002*a*, *b*; 2004) and Canadian (Campanian; Penney 2006*a*) ambers. Wunderlich (2008, p. 57) mentioned Cretaceous Chinese representatives of the Orchestininae, but the reference was to Fu Shun amber, which is Tertiary in age. Almost all described Cretaceous fossil diversity can be attributed to the genus *Orchestina*

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Simon, 1882, which is one of the oldest known lineages among extant spiders (Wunderlich 2004*a*).

The genus *Orchestina* dates back to the Cretaceous and represents the most common and diverse oonopid lineage in the fossil record, with 28 formally described fossil species (Dunlop *et al.* 2011). According to Wunderlich (2008), 10 per cent of Baltic amber spiders may be undescribed *Orchestina* specimens. The first fossil *Orchestina* was described from Baltic amber by Menge (1854) as *Segestria pusilla* (Wunderlich 1981, 2004*a*). The lineage is undoubtedly monophyletic (Saaristo 2001; PBI 2010) and is diagnosed primarily on the enlarged fourth femur used for jumping (Saaristo 2001; Marusik and Wunderlich 2008; PBI 2010).

Here, we describe four new specimens of the genus *Orchestina* (two new species) based on amber material from the Cretaceous of France and Spain. The specimens were discovered in amber from the (1) Font-de-Benon quarry near the village of Archingeay, Charente-Maritime, France (Perrichot and Néraudeau 2009), and from northern and eastern Spain in the outcrops of (2) Peñacerrada I (= Moraza, Burgos Province; Alonso *et al.* 2000), (3) San Just (Teruel Province; Peñalver *et al.* 2007) and (4) El Soplao (Cantabria Province; Najarro *et al.* 2009). These descriptions add to our knowledge of the diversity of the lineage at a relatively early point in its history.

Two of the *Orchestina* specimens (IGR.ARC-28.2 and CPT-4100) were imaged at the European Synchrotron Radiation Facility (ESRF) on beamlines ID19 and BM5 using propagation phase-contrast X-ray synchrotron microtomography (PPC-SRμCT). Although this technique was originally designed for surveying the palaeobiological content of opaque French Cretaceous amber, the method also allows for nondestructive viewing of minute morphological details that are not visible by conventional methods in translucent samples (Tafforeau *et al.* 2006; Lak *et al.* 2008; Soriano *et al.* 2010). The technique generates three-dimensional reconstructions and can reveal internal structures, if preserved. Here, we detail the first spiders to be formally described using PPC-SRμCT. Microtomographic imaging of spider specimens has been previously applied, but all of these studies used conventional X-ray microtomographic machines (e.g. Dierick *et al.* 2007; Penney *et al.* 2007; Selden *et al.* 2008; Bosselaers *et al.* 2010; Penney *et al.* 2011).

AMBER LOCALITIES

The Archingeay-Les Nouillers locality (herein referred to as Archingeay) is the most fossiliferous Cretaceous French amber deposit (Perrichot *et al.* 2007). The specimen originates from the lowermost of two amber-bearing strata exposed in the Font-de-Benon quarry, i.e. the A1sl-A level *sensu* Batten *et al.* (2010) = A1sl1 *sensu* Néraudeau *et al.* (2002). The dating of A1sl-A remains problematic; it contains dinoflagellate cysts suggesting a latest Albian age (Néraudeau *et al.* 2002; Dejax and Masure 2005), while megaspores recently discovered are more indicative of the early Cenomanian (Batten *et al.* 2010). The deposit is unique in that a large percentage of the inclusions represent litter fauna (Néraudeau *et al.* 2002). Four arachnid orders have been found in Charentes amber, comprising nine per cent of the arthropod inclusions, including 38 individuals of Araneae (Perrichot *et al.* 2007; Perrichot *et al.* 2010). Only one spider has been formally described from the deposit (Saupe and Selden 2009), but others were referred to by Schlüter (1978) and Néraudeau *et al.* (2002), and members of the family Zodariidae were mentioned as being present by Perrichot (2004) and Perrichot *et al.* (2007).

In Spain, there are three Cretaceous basins containing Albian amber: the Central Asturian Depression and the Basque-Cantabrian Basin, which drained to the proto-Atlantic, and the Maestrat Basin, which drained to the Tethys (Delclòs *et al.* 2007; Peñalver and Delclòs 2010). The Maestrat Basin lies to the east with several outcrops, the better known of which is San Just near Utrillas village (Peñalver *et al.* 2007). Two other important outcrops occur in the north of Spain within the Basque-Cantabrian Basin: Peñacerrada I in the north-east (Alonso *et al.* 2000; Delclòs *et al.* 2007) and El Soplao in the north-west (Najarro *et al.* 2009, 2010). All localities are associated with continental to marine environments. The Basque-Cantabrian Basin experienced more marine influences than the Maestrat basin. Sedimentologically, the amber deposits of the Maestrat Basin are associated with fluvial swamps, whereas amber deposits of the Basque-Cantabrian Basin are associated with delta-shore marine environments (see synthesis in Peñalver and Delclòs 2010).

The amber from Álava (Peñacerrada I & II outcrops), Basque-Cantabrian Basin, is well documented, with more than 2300 arthropod inclusions discovered to date (Alonso *et al.* 2000; Peñalver and Delclòs 2010). Araneae make up 2.4 per cent of these inclusions (Delclòs *et al.* 2007). Pollen analysis suggests an early Albian age (Barrón *et al.* 2009; Peñalver and Delclòs 2010). Thus far, two spiders have been formally described: a lagonomegopid (Penney 2006*b*) and an araneid (Penney and Ortuño 2006), while others were figured in the study by Alonso *et al.* (2000) and mentioned in the study by Delclòs *et al.* (2007).

The El Soplao outcrop is early Albian in age and located in the north-western part of the Basque-Cantabrian Basin. The deposit is potentially the largest amber site with arthropod bioinclusions in Spain (Najarro *et al.* 2009, 2010), with more than 400 discovered to date. The tarsal claws and silk of a spider were figured in Najarro *et al.* (2009), but no description was made, making the one herein the first.

The San Just outcrop is middle Albian in age and located in the Maestrat Basin (Oliete sub-basin) in Teruel Province (Peñalver *et al.* 2007; Peñalver and Delclòs 2010). Over 200 inclusions have been discovered thus far. Herein, we formally describe the first spider from San Just, which was figured in Soriano *et al.* (2010). The only other spider-related bioinclusions mentioned from this outcrop include a spider web with trapped prey detailed in the study by Peñalver *et al.* (2006) and a spider figured in the study by Delclòs *et al.* (2007).

MATERIALS AND METHODS

All microtomographic data (original and segmented slices, scan parameters, segmentation files, pictures and animations) are available online in the open-access ESRF palaeontology database (http://paleo.esrf.eu). The 3D models in ABS plastic are deposited with the type material in their respective institutions.

IGR.ARC-28.2 and MCNA-12593 were cut and polished, and CES-013 and CPT-4100 were encased in epoxy resin, prior to being received by the authors. Drawings of CES-013 and MCNA-12593 were carried out under incident and transmitted light with the aid of a camera lucida attached to a Leica M205 C stereomicroscope. Drawings were then inked and scanned into Adobe Photoshop CS4. Photographs of CES-013 and MCNA-12593 were taken using a Canon EOS 5D Mk II camera attached to Leica M205 C and Leica DM2500 M microscopes. Image stacks were merged using Helicon Focus 4.2.1 software (HeliconSoft Ltd.). Measurements for CES-013 and MCNA-12593 were captured with an ocular graticule, and measurements for IGR.ARC-28.2 and CPT-4100 were obtained using the scale provided with the synchrotron imaging. All measurements are in mm.

PPC-SRμCT

IGR.ARC-28.2 and CPT-4100 were imaged at the ESRF in Grenoble, France. IGR.ARC-28.2 was scanned on the ID19 beamline, with a set energy of 20 keV, a propagation distance of 50 mm, voxel size of 0.7 μ and 2000 projections with 0.2 s of exposure time. CPT-4100 was scanned on the BM05 beamline, with a set energy of 20 keV, a propagation distance of 100 mm, voxel size of 1.4 μ and 1500 projections with 2 s of exposure time.

Abbreviations. Terminology used in this paper is after Saaristo and van Harten (2006), although we refer to the structure bearing the opening of the seminal duct as the embolus rather than the sembolus; there is currently little evidence suggesting this structure is not homologous with the seminal duct of higher entelegynes. The embolus is polymorphic within the genus and can be blunt, tapering or bifurcate (Marusik and Wunderlich 2008). The relative proportions of the palpal segments and the embolus shape are considered useful in distinguishing among species of *Orchestina* (Wunderlich 2004*a*).

The bulbus index (ratio of bulbus width to height, BI), embolus index (ratio of bulbus width to embolus length, PBI) and patella index (ratio of male palpal patella width to length, PI) are utilized; these indices are considered helpful in diagnosing and describing *Orchestina* species (Saaristo and van Harten 2006). We introduce two new indices: the embolus characterization index (ratio of length of embolus to width of embolus at base: EI; not to be confused with the PBI) and the tibial index (ratio of palpal tibia width to length), which also may be useful in characterizing male *Orchestina*.

Anatomical abbreviations. Leg formula (e.g. 1423) indicates the length of each leg relative to the other legs from longest to shortest (in the example, 1 is the longest, followed by leg 4). ALE, anterior lateral eyes; ALS, anterior lateral spinneret(s); cx, coxa; cy, cymbium; em, embolus; fe, femur; MS, median spinneret(s); mt, metatarsus; PLE, posterior lateral eyes; PLS, posterior lateral spinneret(s); PME, posterior median eyes; pt, patella; ti, tibia; tr, trochanter; ts, tarsus.

Institutional and collection abbreviations. AMNH, American Museum of Natural History, New York, USA; CES, Colección El Soplao, Cueva El Soplao, Celis, Cantabria, Spain; CPT, Colección Paleontológica de Teruel, Teruel, Spain; ESRF, European Synchrotron Radiation Facility, Grenoble-Cedex, France; GPIMUH, Geological-Palaeontological Institute, University of Hamburg, Hamburg, Germany; MCNA, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; MNHN, Muséum national d'Histoire naturelle, Paris, France; SMNG, Senckenberg Museum für Naturkunde Görlitz, Görlitz, Germany.

Other material examined

Orchestina breviembolus Wunderlich, 1981; ♂ (holotype) from Baltic amber, GPIMUH 2526; ♂ (paratype) from Baltic amber, GPIMUH 2518; ♂ (paratype) from Baltic amber, GPIMUH 2501.

Orchestina colombiensis Wunderlich, 2004*b*; ♂ (holotype) from Colombian copal, SMNG 07136286.

Orchestina forceps Wunderlich, 1981; ♂ (holotype) from Baltic amber, GPIMUH 2524.

Orchestina furca Wunderlich, 1981; ♂♀ (holotype and paratype, respectively) from Baltic amber, GPIMUH 2519+.

Orchestina parisiensis Penney, 2007; ♂ (holotype) from Le Quesnoy amber (Paris Basin, France), MNHN A30090 (=PA 759); ♂ (paratype) from Le Quesnoy amber, MNHN A32049 (=PA 1909 1/3).

Orchestina sp. described in Penney, 2006*a*; juvenile from Burmese amber, AMNH-Bu-706.

Repository. The four specimens described here are deposited in the following institutions: (1) Department of Geosciences at the University of Rennes 1, Rennes, France; (2) Museo de Ciencias Naturales de Álava (MCNA), Vitoria-Gasteiz, Álava, Spain; (3) Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain; and (4) Institutional Collection from the El Soplao outcrop in the Laboratory of the El Soplao Cave, Celis, Cantabria, Spain.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757
Suborder OPISTHOTHELAE Pocock, 1892
Infraorder ARANEOMORPHAE Smith, 1902

Family OONOPIDAE Simon, 1890

Remarks. The monophyly of the Oonopidae was traditionally regarded as uncertain, and only two derived characters, the loss of cheliceral teeth and the loss of the female palpal claw, separated oonopids from other dysderoids (Platnick and Brescovit 1995; Platnick *et al.* 1991). Recently, Burger and Michalik (2010) discovered an additional synapomorphy (males possess an unpaired or completely fused testis) that may support the monophyly of the family.

Genus ORCHESTINA Simon, 1882

Type species. Schoenobates pavesii Simon, 1873, by monotypy. Recent from Spain, southern France, Corsica and Algeria.

Range. Early Cretaceous (early Albian from Spanish amber) to Recent.

Diagnosis. Orchestina belongs within the molles (soft-bodied) subgroup of the Oonopidae; the other subgroup consists of species with strong sclerotization (loricatae; Simon 1893*a*). The division is likely not monophyletic (PBI 2010) but corresponds to the subfamilies Oonopinae Simon, 1890 and Gamasomorphinae Petrunkevitch, 1923, respectively (Saaristo 2001).

The primary character diagnosing the genus *Orchestina* is the enlarged fourth femur, providing the ability to jump (Saaristo 2001). Although undoubtedly monophyletic, some authors have claimed that the group is diagnosed too broadly and is in need of revision (e.g. Saaristo 2001; Wunderlich 2008).

When paired with an enlarged fourth femur, other characters diagnostic for the genus are abdomen high and rounded, sclerotized seminal duct in the palpal bulbus, six eyes in segestriid position ('H' conformation) and the presence of a swollen palpal tibia, which is often wider and larger than the palpal femur (however, one fossil and two extant species do not share this trait; Marusik and Wunderlich 2008). The subfamily Orchestininae, created by Chamberlin and Ivie (1942), has not held up to scrutiny.

Remarks. All studied specimens possess the diagnostic enlarged fourth femur, six eyes in the segestriid position, a raised carapace and a rounded, high opisthosoma, placing them firmly within the genus *Orchestina*.

Orchestina gappi sp. nov.
Figures 1–5

Derivation of name. The specific epithet is after I. Wesley Gapp, a student of palaeontology with a contagious passion for the history of life on Earth.

Material. Holotype and only known specimen IGR.ARC-28.2, male (Figs 1–5); deposited in the amber collection of the Department of Geosciences at the University of Rennes 1, Rennes, France.

Preservation. The specimen is preserved in a piece of dark brown, fairly opaque amber $12 \times 6 \times 3$ in size. Syninclusions included a Psocoptera, a Diptera in the Chironomidae and a Dermaptera in the Pygidicranidae (V. Perrichot, pers. comm. 2010; Perrichot *et al.* 2011), although the piece was subsequently divided into two fragments (numbers ARC-28.1 to ARC-28.2) for optimal study. Only the dorsal side of the spider is visible using conventional methods; thus, PPC-SRμCT was utilized at the ESRF. The specimen is extremely well preserved, with only the opisthosoma suffering from dorso-ventral compression.

Locality and age. Font-de-Benon quarry, 1 km east of Archingeay-Les Nouillers (Charente-Maritime, France); uppermost Albian–lowermost Cenomanian (amber level A1sl-A; Néraudeau *et al.* 2002; Dejax and Masure 2005; Batten *et al.* 2010).

Diagnosis. Orchestina gappi sp. nov. can be distinguished from all other species by the concave shape of the bi-pronged embolus, which flares outward medially, reaching greatest width, and subsequently tapers distally. The longer embolus prong occurs entally. Further diagnostic characters include an ovoid, symmetrical palpal bulb with an embolus that emerges medially and a palpal tibia that bulges proximally.

Description. Body 1.00 long, small in size *sensu* Saaristo (2001), with length of carapace <0.60. Carapace 0.56 long, 0.49 wide, 0.20 wide at ocular region, 0.27 high; circular in outline, elevated into a dome that peaks past midpoint; steeply sloping carapace sides (Fig. 1); 16 setae present dorsally, *c.* 0.07–0.08 long; fovea absent. Clypeus fairly vertical, not sloping outward, 0.08 high; height 1.39× longer than width of PME; no indentations or projections present. Six eyes in segestriid position; subequal in size; PME contiguous with ALE in a row, with PLE above and contig-

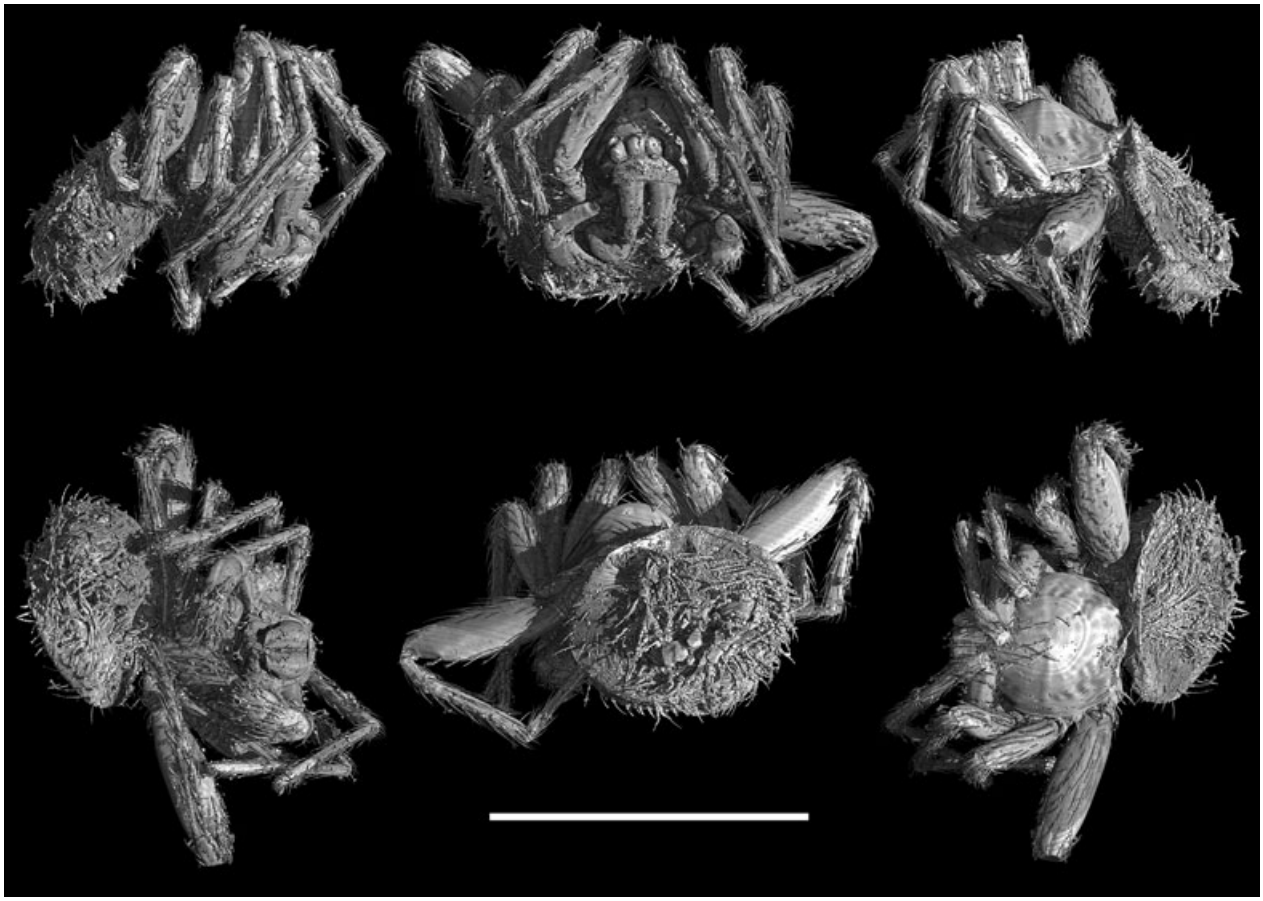

FIG. 1. 3D reconstruction of habitus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, ESRF, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Scale bar represents 1 mm.

uous with ALE; ALE wider than long and ovoid; PME longer than wide, ovoid; PLE kidney-shaped; one long seta projecting above each PLE. Chelicerae short, conical; 0.25 long, 0.10 wide at base; fang short. Labium kidney-shaped, wider than long, 0.10 wide at widest point. Endites cone-like and slender; *c.* 0.12 long, *c.* 0.05 wide; converging but not meeting. Sternum convex, heart-shaped with a blunt posterior end; *c.* 0.19 long, 0.32 wide at broadest point; no visible indentations near endites; approximately 14 setae present. Opisthosoma flattened dorso-ventrally, but probably ovoid to roundish in life; approximately 0.63 long, 0.70 wide; clothed in long setae about 0.09 long; no sclerites present. Six spinnerets positioned slightly ventro-anteriorly (Fig. 2); ALS and PLS divided into two, possibly three segments; ALS longer and wider than PLS, with MS smallest; right ALS 0.15 long, 0.06 wide; left ALS 0.12 long, 0.05 wide; right PLS 0.10 long, 0.03 wide; left PLS 0.09 long, 0.03 wide; right MS 0.07 long, 0.01 wide; left MS 0.09 long, 0.01 wide.

Leg formula 1423/4123; leg 1 cx 0.17, tr 0.07, fe 0.43, pt 0.16, ti 0.38, mt 0.40, ts 0.22, total 1.83; leg 2 cx 0.11, tr 0.06, fe 0.42, pt 0.16, ti 0.33, mt 0.40, ts 0.22, total 1.70; leg 3 cx 0.12, tr 0.06, fe 0.34, pt 0.14, ti 0.26, mt 0.30, ts 0.18, total 1.40; leg 4 cx 0.12, tr 0.06, fe 0.56, pt 0.18, ti 0.35, mt 0.35, ts 0.19, total 1.81. Leg 3 directed forward as in segestriids. Femur 4 enlarged; 1.3× longer than the average of the other femora and 1.58× broader than fe 3 (Fig. 1). Tarsal claws on distinct onychium; claws + onychium 0.05 long; claws with fine teeth. Legs clothed in simple setae, 0.06–0.09 long; apparently no spines present; serrate setae (if present) and trichobothria not visible because of the resolution used for synchrotron imaging.

Palpal segments; cx 0.05 long; tr 0.04 long; fe 0.14 long, 0.06 wide; pt 0.10 long, 0.09 wide; ti 0.17 long, 0.11 wide at broadest point; cy 0.13 long, 0.09 wide at broadest point. PI 0.89; TI 0.65; BI 0.62; PBI 0.83; EI 2.38. Femur fairly slender. Pt swollen. Ti swollen throughout, bulging proximally, covered with long setae, but not as dense as present on cy; trichobothria not visible because of the resolution used for synchrotron imaging. Cymbium triangular in shape with rounded corners, border visible; covered in elongated setae 0.07–0.10 long; cy fully covered by palpal bulb, with possible exception of most proximal part of cy; bulb inserted on ventral side of cy. Palpal bulb ovoid in shape, 0.16 high, 0.10 wide; width of bulb approximately equivalent to the width of ti at widest point (Figs 3–5). Embolus distinct from bulb, emerging almost medially from bulb in relation to where cy attaches; thick at base and throughout; 0.12 long, 0.05 wide at base, 0.06 wide at broadest point; structure concave half circle (i.e. curving upward); flaring out medially, particularly on ental side, in a quasi cup or diamond shape, and subsequently thinning; em bifurcated at tip, 0.03 wide at bifurcation, with two subcontiguous prongs; longer prong on ental side, 0.04 long; shorter prong 0.03 long (Figs 4–5).

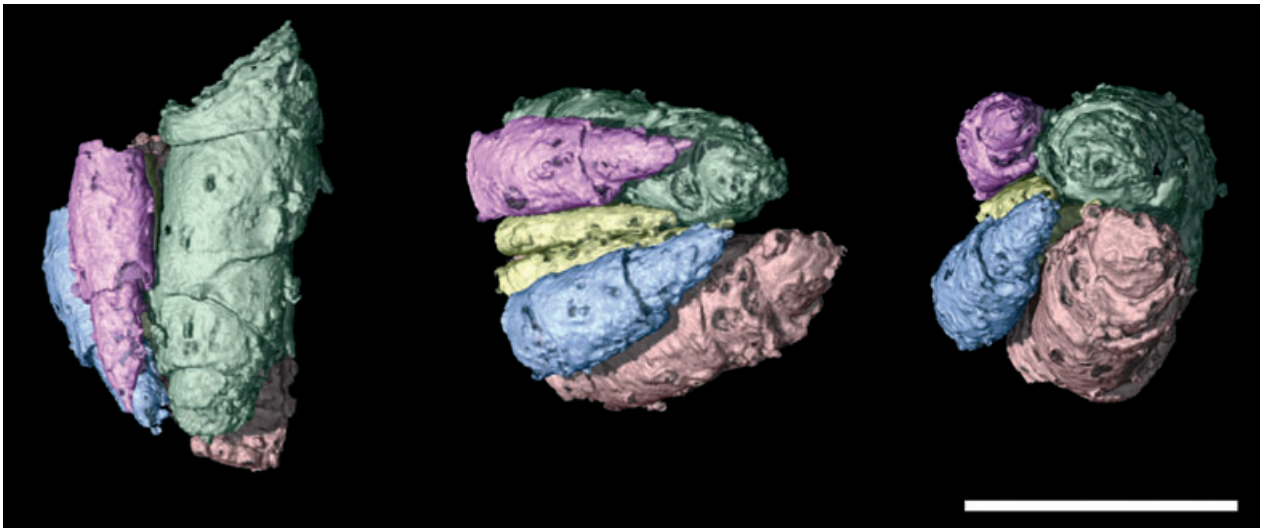

FIG. 2. 3D reconstruction of the spinnerets of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Scale bar represents 100 μm.

Female. Unknown.

Remarks. No other species possess a bi-pronged, diamond-shaped embolus (i.e. flaring medially and curved upwards). Most *Orchestina* species have an embolus that is beak-shaped/convex (a notable exception is *O. parisiensis* from lowermost Eocene Le Quesnoy amber, but this species does not have an embolus that flares medially, and *O. manicata* Simon, 1893*b*, which possesses a pair of black apical dents on the embolus that are missing in *O. gappi* sp. nov.). Further, the palpal bulb of *O. gappi* sp. nov. is egg-shaped and symmetrical, with the embolus emerging medially. Other bulbs are lop-sided, triangular or otherwise shaped, with the embolus emerging from various positions. For example, *O. rabagensis* sp. nov. (this paper) has an embolus that emerges from the bulb distally. The tibial conformation of *O. gappi* sp. nov. is unique when in combination with the above characters: it bulges proximally and tapers distally, whereas other tibiae within *Orchestina* bulge throughout or distally.

Orchestina rabagensis sp. nov.
Figures 6, 7

Derivation of name. The specific epithet is after Rábago, the municipality in Cantabria (Spain) where the El Soplao outcrop is located.

Material. Holotype and only known specimen CES-013, male (Figs 6, 7); housed in the Institutional Collection from the El Soplao outcrop in the Laboratory of the El Soplao Cave, Celis, Cantabria (Spain).

Locality and age. El Soplao outcrop, Cantabria, Spain, early Albian (Najarro *et al.* 2009, 2010).

Preservation. The spider is preserved in a piece of clear, light yellow amber embedded in epoxy resin, $6 \times 6 \times 2$ in size. A platygastrid (parasitoid) wasp is present as a syninclusion. The specimen is complete with the exception of left legs I and II, which are cut at the tibiae. The cuticle is cleared in most of the specimen, with shrunken black remains within. The appendages are compressed, and the eyes and opisthosoma are shrivelled. The cuticle is pitted and particularly mesh-like on the palpal bulb. Barring this, the specimen is well preserved.

Diagnosis. Orchestina rabagensis sp. nov. can be distinguished from all other species by the combined presence of (1) a thin, relatively straight to slightly concave embolus with two long prongs widely separated from each other; (2) longer prong of the embolus positioned ectally; (3) embolus emerging from the bulb distally in relation to the cymbium; and (4) palpal tibia bulbus throughout.

Description. Body *c.* 1.10 long, small in size *sensu* Saaristo (2001), with the length of carapace <0.60. Carapace 0.56 long, *c.* 0.30 high, width not measurable; carapace probably oval in outline, moderately elevated into a dome that peaks at 2/3 of carapace length, resulting in the posterior carapace margin distinctly steeper than the anterior margin; steeply sloping carapace sides; *c.* 15 elongated setae present dorsally, 0.12 long; fovea absent (Fig. 6). Clypeus short, gently sloping forward, 0.04 long; indentations or projections not apparent. Six eyes, most likely in segestriid position, PME contiguous with ALE in a row, with PLE above and contiguous with ALE; eye morphology and measurements uncertain because of the preservation, though eyes similar in size; one long setae projecting above each PLE, 0.12

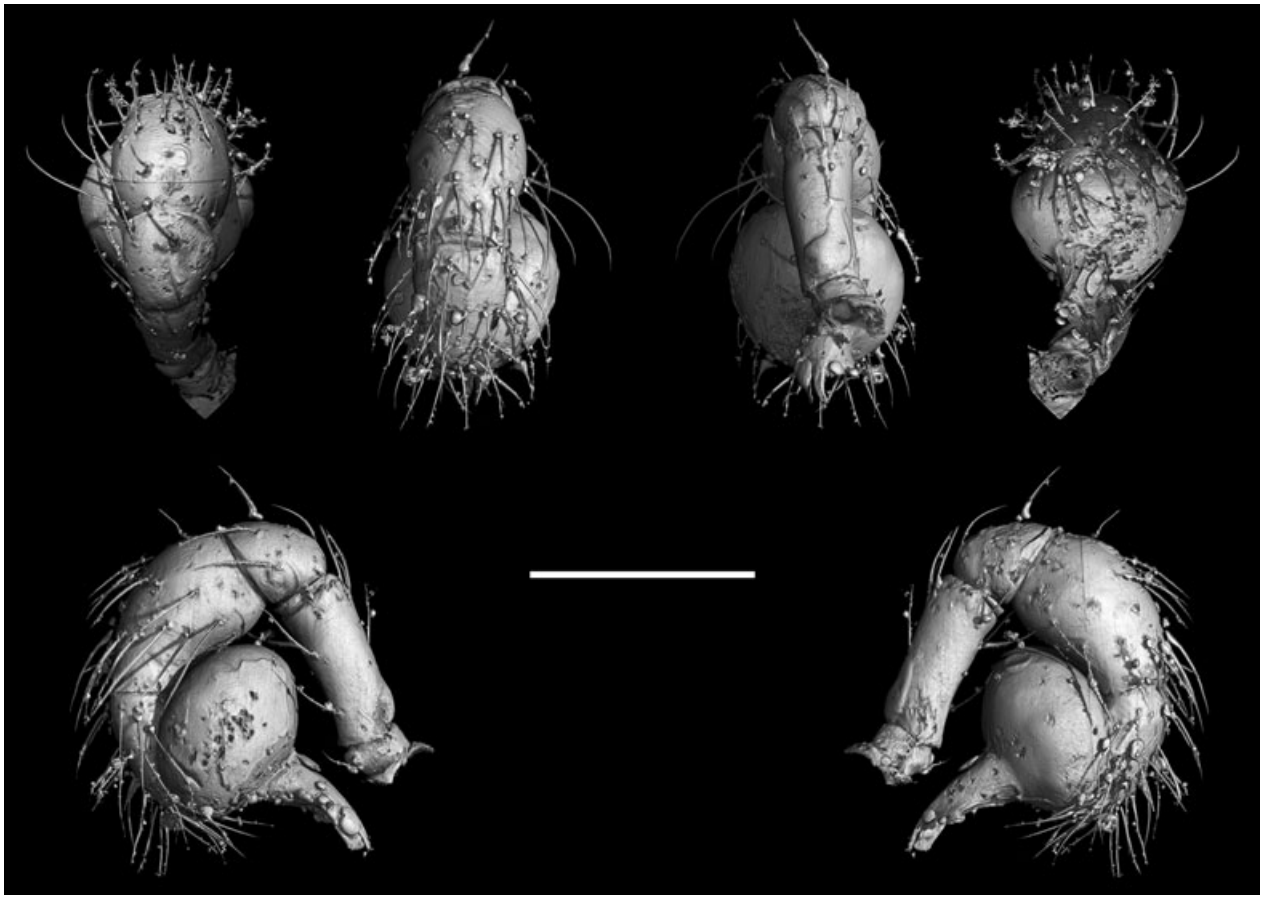

FIG. 3. 3D reconstruction of the left palpus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Lateral, ventral and dorsal views. Scale bar represents 200 μm.

long. Chelicerae short, tapering distally; 0.17 long, width not measurable; fang not visible. Labium, endites and sternum not visible. Opisthosoma morphology uncertain because of the preservation, but probably oval/drop-shaped; 0.52 long, 0.23 wide, 0.23 high as preserved; clothed in setae of about 0.07 length; apparently no sclerites present. Spinnerets not visible.

Leg formula 4213/2413; leg 1 cx 0.06, tr 0.05, fe 0.40, pt 0.15, ti 0.43, mt 0.33, ts 0.24, total 1.66; leg 2 fe 0.49, pt 0.15, ti 0.48, mt 0.36, ts 0.24, total 1.72 (cx and tr unknown); leg 3 fe 0.43, pt 0.12, ti 0.26, mt 0.31, ts 0.22, total 1.34 (cx and tr unknown); leg 4 cx 0.04, tr 0.04, fe 0.58, pt 0.15, ti 0.37, mt 0.45, ts 0.18, total 1.81. Possible space between cx 3 and 4. Femur 4 enlarged, 1.27× longer than the average of the other femora and approximately 1.3–1.4× broader than fe 3 (exact ratio not measurable as the other femora show compression). Tarsal claws on pronounced onychium; claws + onychium 0.06 long; claws with fine teeth. Legs clothed in setae 0.06–0.07 long; particularly elongated setae present in distal part of all fe, up to twice as long as other setae; serrate setae present on all mt and ts, serration more apparent on ts, also present on pt and ti of leg 4; short, rather thin spine on distalmost portion of fe 4. Trichobothria very elongated, up to 0.12–0.14 long, distinctly feathery (Fig. 7A), dorsally on ti and mt as follows: (1) one on 6/10 parts of ti 1 + 2; (2) two on ti 3, one on 1/5 parts and another on its midlength; (3) three on ti 4, close together along 3/5 of its length; and (4) one on almost distal tip of all mt. Tactile setae present, erect, short (0.03–0.04 long), not distinctly feathery, located dorsally and ventrally on ti, mt and ts (Fig. 7A), when occurring ventrally often arranged in pairs on mt and ts; longer tactile setae, 0.06–0.07 long, present dorsally on distal tip of ts 1 + 2.

Palpal segments; cx 0.04 long; tr 0.04 long, 0.04 wide; fe 0.11 long, 0.05 wide; pt 0.11 long, 0.05 wide at broadest point; ti 0.11 long, 0.08 wide; cy 0.08 long, 0.07 wide at broadest point. Palp laterally compressed so palpal indices may be misleading: PI 0.41; TI 0.73; BI 1.11; PBI 0.90; EI not determinable because width of em not measurable. Femur fairly slender. Patella appears elongate and thin. Tibia enlarged, bulbus throughout without tapering distally or proximally; covered with long setae but not as dense as in cy; one long trichobothria dorsally on midlength. Cymbium broad as preserved, triangular in shape with rounded corners, border visible; covered in elongated setae 0.09 long; cy fully covered by palpal bulb; bulb inserted on ventral side of cy. Palpal bulb likely ovoid in shape (shape distorted owing to lateral compression), 0.10 long, 0.09 wide; bulb cuticle particularly net-like. Embolus emerging more distally on bulb in relation to where cy attaches; thicker at base and tapering towards a bifurcating point (Fig. 7B); 0.11 long, 0.03 wide at base; em fairly straight, although curved slightly upward especially at tip (i.e. concave); em bifurcated slightly after

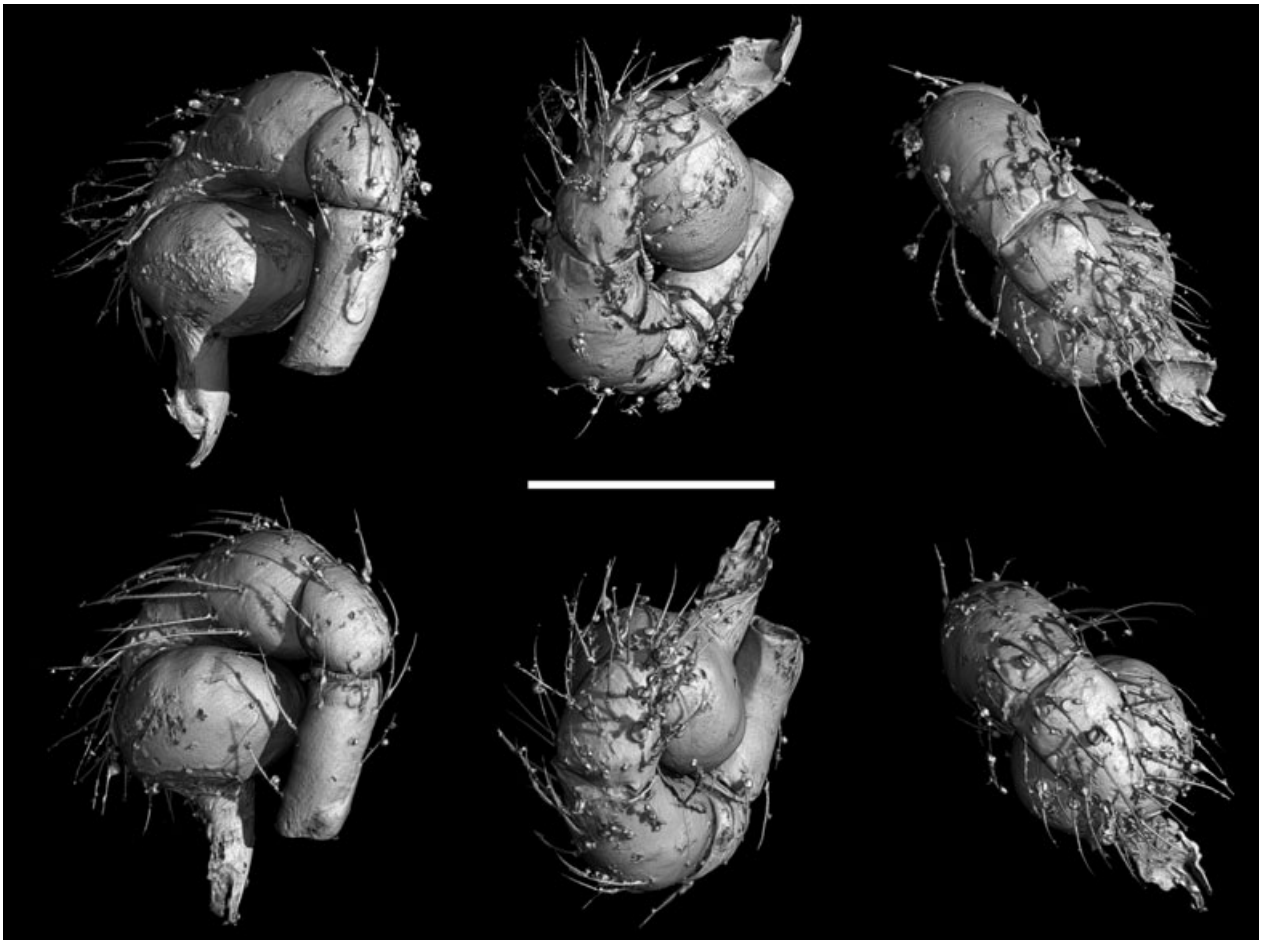

FIG. 4. 3D reconstruction of the left palpus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Oblique and dorsal views. Scale bar represents 200 μm.

its midpoint, 0.01 wide at bifurcation, with two prongs widely separated; longer prong on ectal/outer side, 0.05 long.

Female. Unknown.

Remarks. The widely separated prongs on a thin, tapering embolus are unique among *Orchestina*. Of the bi-pronged *Orchestina* species, none exhibit such a wide angle between the prongs and also possess such a dramatically tapering and relatively straight embolus (i.e. without kinks). *Orchestina colombiensis*, for example, has a long, thin embolus with two prongs, but the prongs are short and subequal in length. *Orchestina furca* possesses uneven prong lengths, but again, they are not widely spaced and the embolus is kinked (convex), not straight to slightly concave. A similar situation exists with *O. forceps*, while *O. longimana* Wunderlich, 1981 possesses widely spaced prongs, but the embolus is not tapering and emerges medially from the palpal bulb, not distally. It is interesting to note that the cymbium is much broader in *O. rabagensis* sp. nov. than in *O. gappi* sp. nov.

Orchestina sp. 1
Figures 8, 9

2010 *Orchestina* sp. Soriano *et al.*, fig. 4.1.

Material. CPT-4100, female deposited in the Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain.

Preservation. The specimen is preserved in a clear orange amber piece embedded in epoxy resin, 5 × 3 × 1.5 in size. Prosoma and opisthosoma are obliquely distorted, with the latter laterally crushed. The left and right legs are oriented in two subparallel planes. Abundant minute bubbles surround the opisthosomal setae and those leg segments in close contact. A coiled spider-web thread and a trichome are preserved as syninclusions.

Locality and age. San Just outcrop, Teruel, Spain, middle Albian (Delclòs *et al.* 2007; Peñalver *et al.* 2007; Peñalver and Delclòs 2010).

Description. Body 1.11 long, small in size *sensu* Saaristo (2001), with the length of carapace <0.60. Carapace 0.44 long, 0.35 wide,

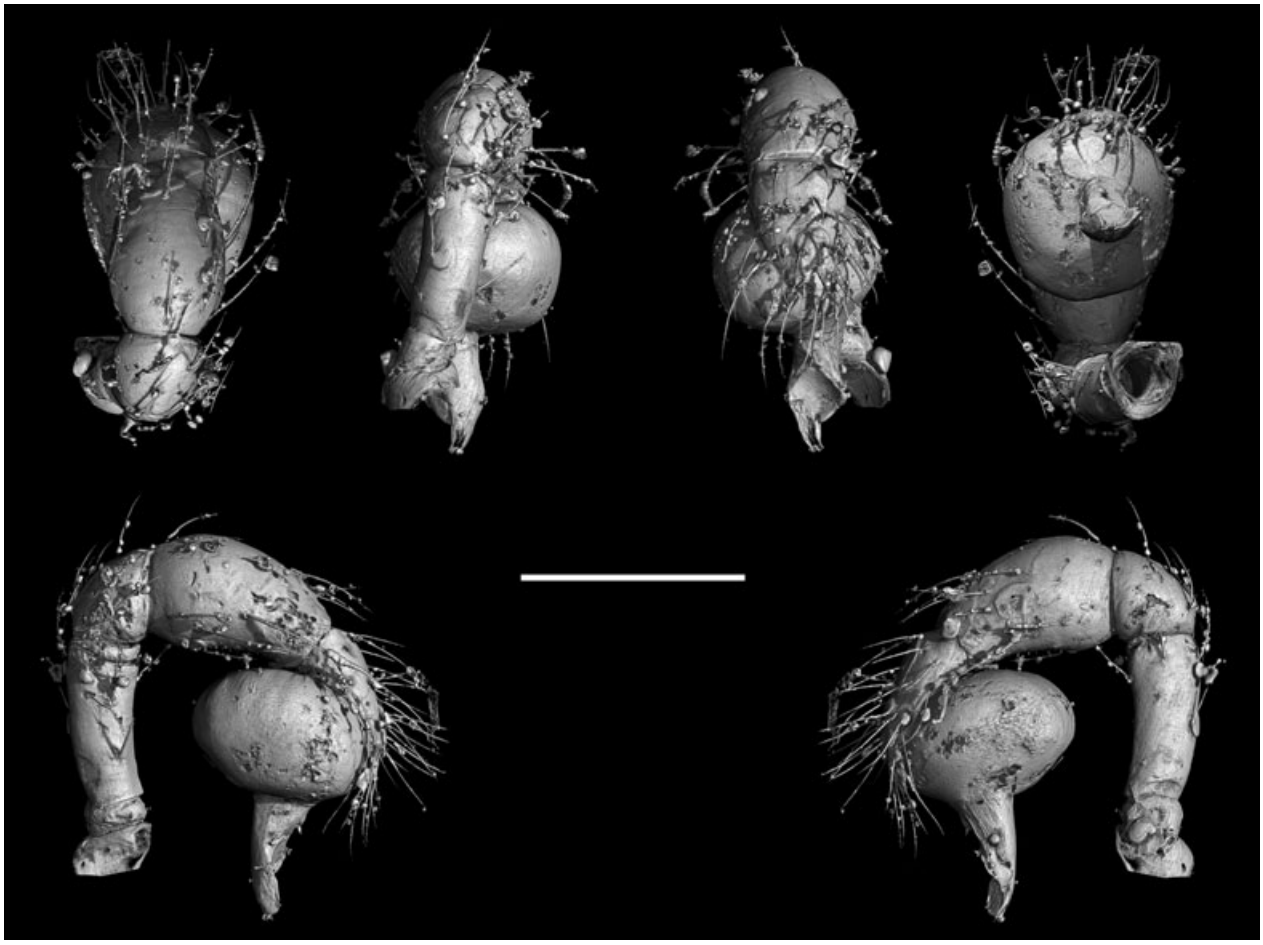

FIG. 5. 3D reconstruction of the right palpus of *Orchestina gappi* sp. nov., holotype IGR.ARC-28.2, from the Font-de-Benon quarry, Archingeay-Les Nouillers (Charente-Maritime, France). Lateral, ventral and dorsal views. Scale bar represents 200 μm.

0.17 wide at ocular region, 0.23 high; oval in outline, elevated into a dome that peaks at 2/3 of carapace length, resulting in the posterior carapace margin distinctly steeper than the anterior margin; steeply sloping carapace sides (Figs 8, 9); *c.* 20 elongated setae present dorsally, placed from behind the top of the carapace to above the eyes, 0.14 long. Clypeus fairly vertical, not sloping outwards, moderately short, 0.04 high; height 1.27× shorter than width of PME; no indentations or projections present. Six eyes in segestriid position; PME contiguous with ALE in a row, with PLE above and contiguous with ALE; PME eyes ovoid, 0.06 long, 0.06 wide; ALE almost circular, 0.06 long, 0.06 wide; PLE twisted so they appear more rhomboid shaped, 0.05 wide, 0.06 high. Chelicerae short, conical; 0.18 long, 0.08 wide at base; fang fairly short. Labium fan or delta-shaped, broader than long; 0.11 wide at widest point; with two subparallel lines dividing labium into three parts, central part slightly larger than laterals. Endites long and thin; 0.10 long, 0.04 wide; converging but not meeting. Sternum fairly convex, faintly heart-shaped but with a blunt distal end; 0.30 long, 0.30 wide at widest point; with slight projections between coxae; several setae present, 0.05–0.06 long. Opisthosoma bulbous and oval with an anterior-dorsal peak; 0.67 long (measured to tip of spinnerets), 0.38 wide at broadest point, 0.50 high at maximum height; clothed in long setae about 0.08–0.09 long; no sclerites present. Six spinnerets; ALS and PLS divided into at least two segments; ALS thickest and longest, 0.10 long, 0.04 wide; MS thinnest, 0.10 long, 0.01 wide; PLS 0.08 long, 0.03 wide.

Leg formula 4213/4123; leg 1 cx 0.10, tr 0.05, fe 0.36, pt 0.14, ti 0.28, mt 0.26, ts 0.22, total 1.41; leg 2 cx 0.10, tr 0.05, fe 0.36, pt 0.15, ti 0.28, mt 0.27, ts 0.21, total 1.42; leg 3 cx 0.10, tr 0.04, fe 0.31, pt 0.14, ti 0.22, mt 0.23, ts 0.19, total 1.23; leg 4 cx 0.12, tr 0.05, fe 0.40, pt 0.17, ti 0.27, mt 0.28, ts 0.19, total 1.48. Leg 3 projected forward as in segestriids with space between cx 3 and 4 (NB: only appears as such on left side). Femur 4 enlarged, 1.18× longer than the average of the other femora and 1.4× broader than fe 3. Tarsal claws on pronounced onychium; claws + onychium 0.06 long; claws with fine teeth. Legs clothed in setae 0.08–0.10 long, particularly elongated setae present on distal part of all fe, up to 0.14 long; serrate setae present on mt and ts, serration more apparent in ts; short, rather thin spine on distalmost portion of fe 4. Trichobothria elongated, about 0.10 long; distinctly feathery; dorsally on ti and mt as follows: (1) one on 6/10 parts of ti 1 + 2; (2) two on ti 3, close together along 3/5 of its length; (3) three on ti 4, close together along

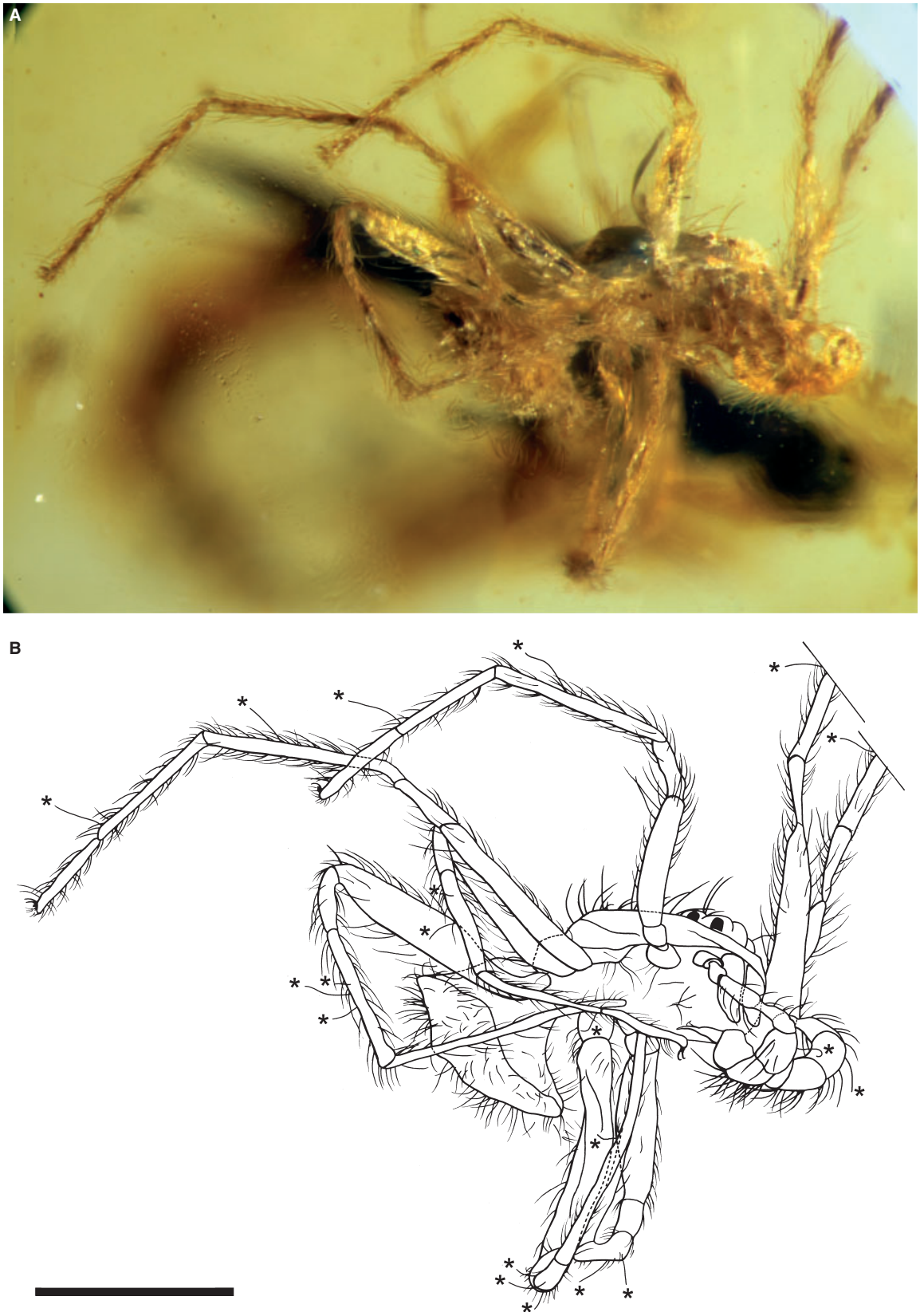

FIG. 6. *Orchestina rabagensis* sp. nov., holotype CES-013, from the El Soplao outcrop, Cantabria, Spain. A, lateral habitus. B, interpretive drawing, with stars representing noted trichobothria. Scale bar represents 0.5 mm for both images.

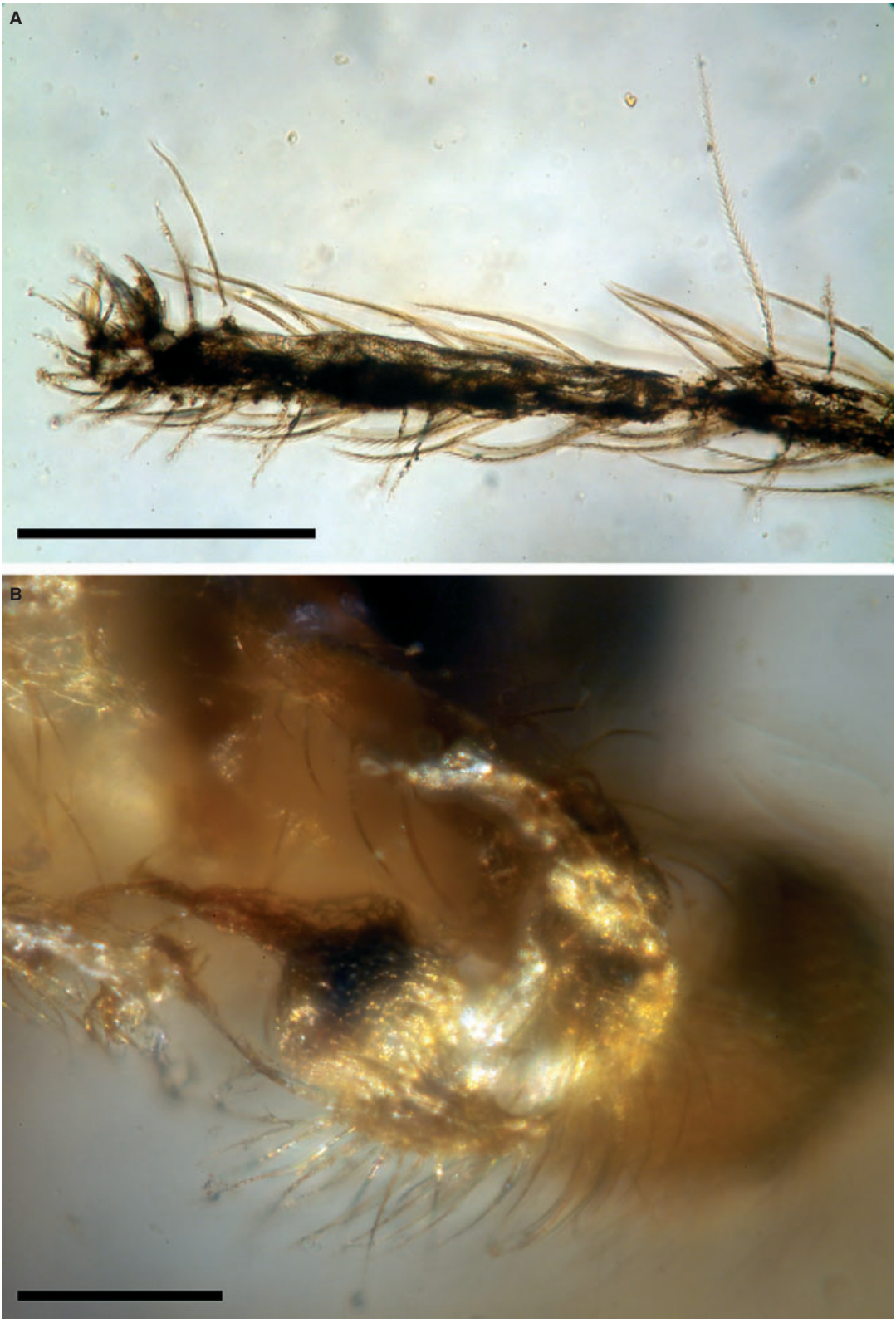

FIG. 7. *Orchestina rabagensis* sp. nov., holotype CES-013, from the El Soplao outcrop, Cantabria, Spain. A, tarsus and part of metatarsus. Note the elongated, feathery trichobothria on the distal portion of the mt, as well as the relatively short, erect, tactile setae on the ventral and dorsal ts and mt. B, lateral view of right palpus. Note the mesh-like appearance of the palpal bulb, likely a preservational artefact, and the long, divided embolus. Scale bars represent 0.1 mm.

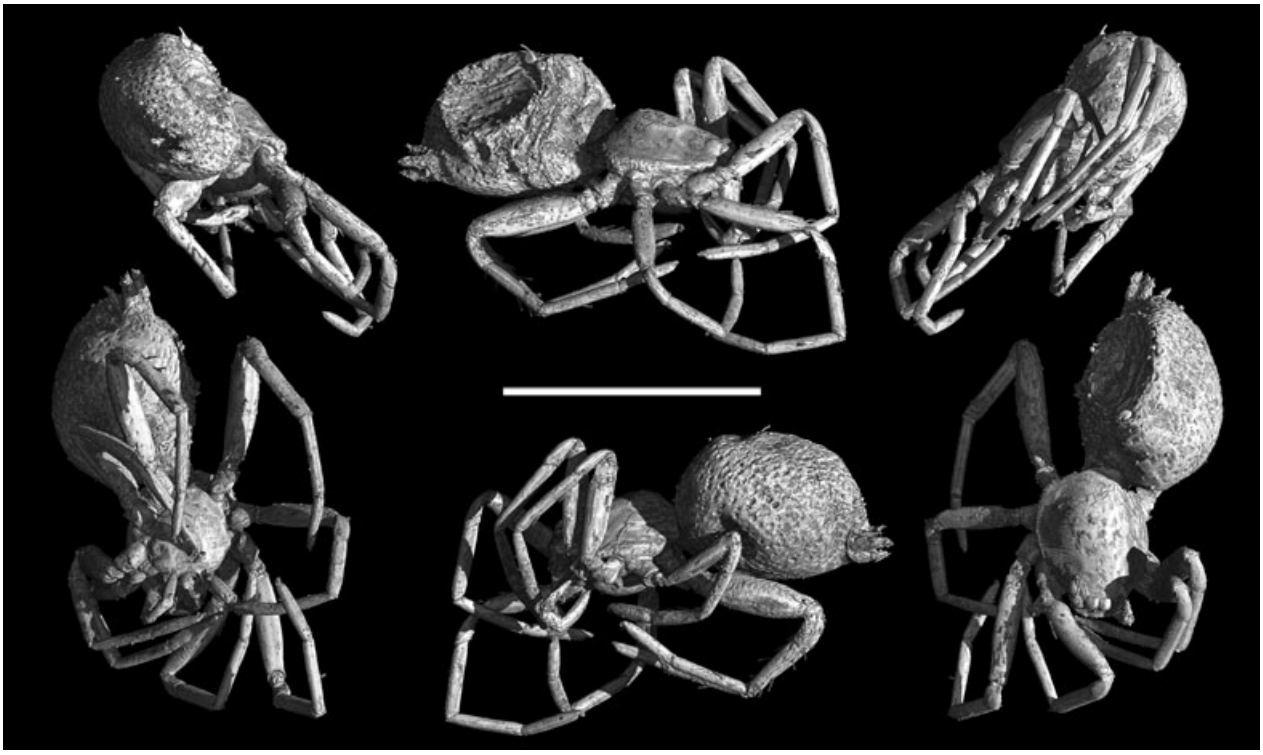

FIG. 8. 3D reconstruction of habitus of *Orchestina* sp. 1 (CPT-4100) from the San Just outcrop, Teruel, Spain. Scale bar represents 1 mm.

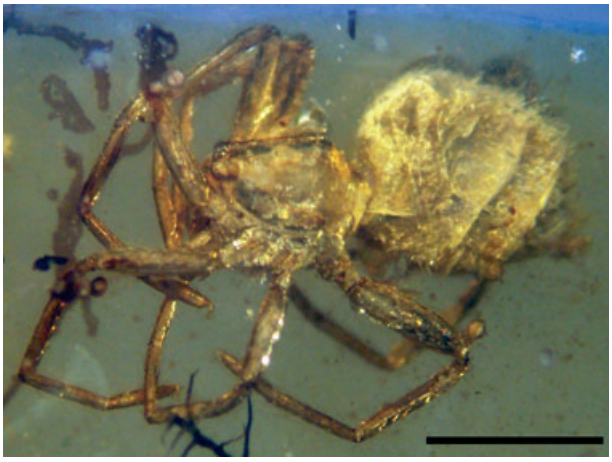

FIG. 9. Lateral habitus of *Orchestina* sp. 1 (CPT-4100) from the San Just outcrop, Teruel, Spain. Scale bar represents 0.5 mm.

3/5 of its length; and (4) one on almost distal tip of all mt. Some tactile setae present, erect, short (0.03 long), not distinctly feathery, located ventrally, a few on distal mt and a few pairs on ts of legs 1 + 2; longer tactile setae, 0.05 long, present dorsally on distal tip of all ti, mt and ts.

Palpus slender; cx 0.10 long; tr 0.02 long; fe 0.10 long; pt 0.08 long, 0.04 wide; ti 0.07 long, 0.04 wide; ts 0.16 long. Trichobothria not visible.

Orchestina sp. 2
Figure 10

Material. MCNA-12593, female; deposited in the Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Álava, Spain.

Preservation. The specimen is embedded in a piece of clear, dark orange amber 12 × 6 × 1 in size. The amber is slightly clouded by organic debris. The spider is almost complete, with left leg 2 (possibly 1?) absent and the opisthosoma dorsally collapsed. The anterior left leg 1 (2?) is disarticulated and in connection with the anterior carapace. The legs exhibit different degrees of compression, although left femur 4 does not appear to be affected. A longitudinal amber fracture runs along the top of the carapace and one leg, whereas another crosses the ventral part of the opisthosoma. The specimen is preserved in fronto-dorsal view, and thus, the ventral characters of the prosoma are not currently visible. A thread of silk emerges from the right ALS.

Locality and age. Peñacerrada I (= Moraza) outcrop, Burgos, Spain, early Albian (Alonso *et al.* 2000; Delclòs *et al.* 2007; Peñalver and Delclòs 2010).

Description. Body length not measurable, but >1.00. Carapace length not measurable, 0.42 wide, 0.22 high at maximum height; ocular region width not measurable; carapace elevated into a dome that peaks at 2/3 of carapace length, resulting in the posterior carapace margin distinctly steeper than the anterior

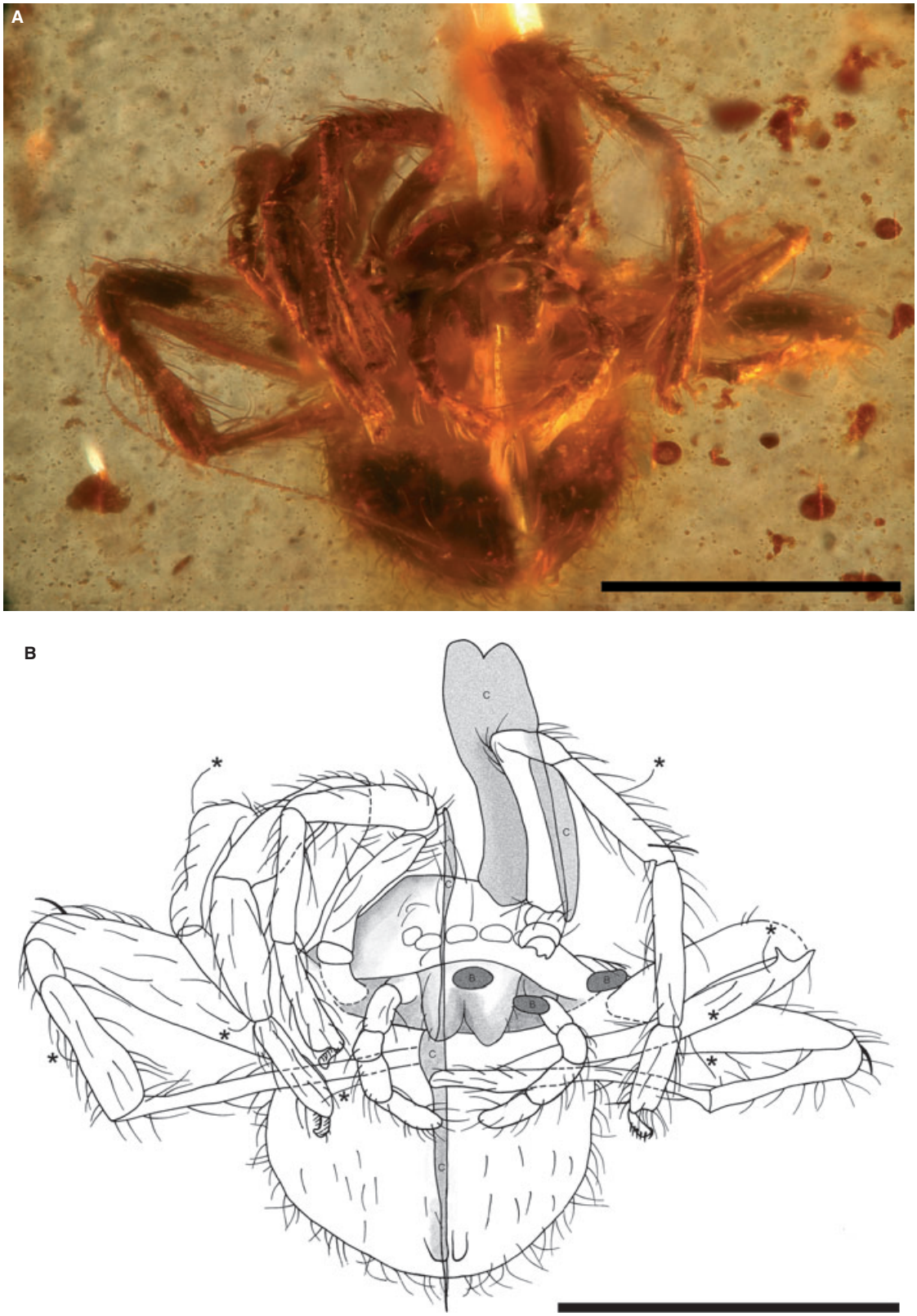

FIG. 10. *Orchestina* sp. 2 (MCNA-12593) from the Peñacerrada I outcrop (= Moraza), Burgos, Spain. A, frontal habitus. Note the silk thread emerging from the spinnerets to the left of the image. B, interpretive drawing with stars indicating known trichobothria. C = crack, B = bubble. Scale bars represent 0.5 mm.

margin; posterior margin probably concave (although crushed); steeply sloping carapace sides; at least eight setae present dorsally, 0.10 long; fovea not visible. Clypeus with a low slope, projecting outward, height not measurable; no indentations or projections present. Six eyes in segestriid position; PME contiguous with ALE in a row, with PLE above and contiguous with ALE; PME the largest, 0.05 wide, 0.03 high; ALE slightly smaller and more rounded than PME, 0.05 wide, 0.03 high; a few long setae present above ocular area. Chelicerae short, conical; 0.13 long, 0.05 wide at base; fang stout, length not measurable. Labium, endite and sternum not visible. Opisthosoma ovoid to rounded in shape; 0.50 long, 0.50 wide at maximum width; clothed in rather short setae of about 0.05 long; no sclerites present. Spinnerets positioned ventro-anteriorly; ALS longest and widest, length not measurable, 0.03 wide; PLS and MS difficult to discern.

Leg formula 4213; leg 1 cx 0.04, tr 0.02, fe 0.23, pt 0.05, ti 0.26, mt 0.21, ts 0.19, total 1.00; leg 2 fe 0.30, ti 0.25, mt 0.22, ts 0.19, total 0.96 (cx, tr and pt unknown, but if these lengths were considered, the total length would exceed leg 1 length); leg 3 fe 0.23, ti + mt + ts 0.50, total 0.73 (cx, tr and pt unknown); leg 4 fe 0.45, pt 0.08, ti 0.22, mt + ts 0.48, total 1.23 (cx and tr unknown). Femur 4 enlarged, 1.78× longer than the average of the other femora and approximately 1.5× broader than fe 3 (exact ratio not measurable as long as fe 3 shows compression). Tarsal claws on pronounced onychium; claws + onychium 0.05 long; claws with fine teeth. Legs clothed in setae 0.07–0.10 long; distinctly longer setae present on ventral side of ti 4, 0.08–0.09 long; serrate setae present on mt and ts, serration more apparent on ts; short, rather strong spine on distalmost portion of fe 4. Trichobothria very elongated, 0.12 long, distinctly feathery, dorsally on ti and mt as follows: (1) one on 6/10 parts of ti 1 (=ti 2?); (2) three on ti 3, one proximal, one medial and another distal; (3) one on midlength of ti 4; (4) one probably on distal mt 3; and (5) one on the distalmost tip of mt 1 (=mt 2?) and mt 3. A few tactile setae present, erect, short (0.04 long), not distinctly feathery, visible on distal ti 1 (=ti 2?) and at midlength of mt 1 (=mt 2?).

Palpus relatively stout; constant width throughout segments, 0.05 wide; fe 0.08 long, pt 0.05 long, ti 0.07 long, ts 0.12 long. One long trichobothria present dorsally at 4/10 parts of ti. Concentrated setae on distal end of palpal tarsus.

Remarks. We posit that CPT-4100 and MCNA-12593, both females and thus difficult to diagnose at species level, are not conspecific based on the following characters: the clypeus in CPT-4100 is vertical, whereas the clypeus in MCNA-12593 projects outward with a low slope. Other differences arise in setation; longer setae are present on the ventral side of ti 4 in MCNA-12593, while this trait is present on the ventral, distal ends of all femora in CPT-4100. MCNA-12593 possesses concentrated setae on the distal end of the palpal tarsus, but this character is absent in CPT-4100.

DISCUSSION

The exact relationships among species within the genus *Orchestina* have not been elucidated, and the group would benefit from phylogenetic analysis, particularly when combining extant and extinct diversity. Performing this sort of analysis at present, however, is not prudent when described species represent perhaps only 20 per cent of the true family diversity (PBI 2010). The Oonopid Planetary Biodiversity Inventory (PBI) is working towards more fully characterizing the family (PBI 2010), so this situation may soon change.

The two new species described herein seem to resemble those within the *O. pavesii* Group as designated by Marusik and Wunderlich (2008). According to these authors, this group includes the fossil species *O. forceps*, *O. furca* and possibly *O. colombiensis*; the extant species *O. pavesii*, *O. arabica* Dalmas 1916, *O. pavesiiformis* Saaristo, 2007, *O. manicata*, and four questionable species *O. bedu* Saaristo and van Harten, 2002, *O. mirabilis* Saaristo and van Harten, 2006, *O. hammamali* Saaristo and van Harten, 2006, and *O. lahj* Saaristo and van Harten, 2006. A bifid embolus tip seems to be the only diagnostic character supporting this assignment, which is potentially problematic as other species display this feature and were placed in different groups by Marusik and Wunderlich (2008).

Wunderlich (2008) erected two new genera for specimens described as *Orchestina* in Canadian and Burmese ambers. More specifically, he transferred the *Orchestina* species Penney (2006*a*) described from Cretaceous Canadian amber to *Canadaorchestina* Wunderlich, 2008. According to Wunderlich (2008), the undescribed Cretaceous New Jersey *Orchestina* mentioned by Penney (2002*b*, 2004) may also fall within *Canadaorchestina*. In the same volume, Wunderlich (2008) erected a new genus for those *Orchestina* found in Burmese amber, namely *Burmorchestina* Wunderlich, 2008; the Burmese specimen mentioned in Penney (2000) is considered a paratype of the monotypic species *B. pulcher* Wunderlich, 2008, but the undescribed *Orchestina* in Burmese amber of Penney (2006*a*) was not mentioned.

Neither *O. gappi* sp. nov. nor *O. rabagensis* sp. nov. place within Wunderlich's (2008) two new genera. Diagnostic characters for *Canadaorchestina* include slender palpal segments, a slender elongated bulbus and a long, thin, undivided embolus. As discussed, *O. gappi* sp. nov. and *O. rabagensis* sp. nov. have enlarged palpal segments, rounded bulbs and divided emboli. Similarly, diagnostic characters for *Canadaorchestina* include slender palpal articles and a large conductor on the palp, neither of which our specimens possess.

Whether Wunderlich's (2008) genera are valid is a matter of contention. While many have indicated the need for further division of the genus *Orchestina* (e.g. Saaristo 2001; Saaristo and Marusik 2004 with the creation of *Ferchestina*), the suggested diagnostic characters and rationale presented by Wunderlich (2008) are not especially convincing. The slender palpal articles are perhaps the

most striking character of both genera, but whether this warrants genus-level status is debatable. Further, because the Oonopid PBI will shed light on relationships within *Orchestina*, it might be best to refrain from subdivision until research within the group is further along. As it stands, the monotypic genera Wunderlich (2008) created are potentially paraphyletic and, if so, are not evolutionarily interesting.

CONCLUSIONS

The newly detailed palaeodiversity may significantly aid with the Oonopid PBI; first, because the specimens presented herein are among the oldest described oonopids, with the Spanish amber representatives being the oldest to date; and second, because according to the fossil record and as indicated by the eye pattern (PBI 2010), *Orchestina* may be the basalmost lineage of the family. The genus was already diverse and widespread by the Cretaceous, with recognized representatives in ambers from Spain (this paper), Myanmar (Penney 2006*a*), France (this paper), New Jersey (Penney 2002*b*, 2004) and potentially Canada (Penney 2006*a*).

In addition to providing information on the past biodiversity of this old group, we illustrate the utility of PPC-SRμCT imaging for studying minute details of specimens preserved in amber. The technique is particularly useful when analysing delicate characters with taxonomic importance (i.e. the male palps) and for unlocking details of specimens once partially or wholly obscured. The anatomical position of the spider itself often conceals vital characters such as the palp, sternum, labrum, endites and petiole, and thus, PPC-SRμCT is invaluable for revealing full character suites in these and similar situations.

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