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New lagonomegopid spiders (Araneae: †Lagonomegopidae) from Early Cretaceous Spanish amber

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Four new species belonging to the enigmatic fossil spider family Lagonomegopidae Eskov & Wunderlich, 1995 are described from Albian Spanish amber. Two new genera are created: *Spinomegops* gen. nov., based on two specimens described as *S. arcanus* sp. nov. from Álava amber (Peñacerrada I outcrop, Burgos), and *S. aragonensis* sp. nov. from San Just amber (Teruel); and *Soplaogonomegops* gen. nov., represented by the type species *S. unzuei* sp. nov. from El Soplao amber (Cantabria). A single specimen from Álava amber is tentatively assigned to *Lagonomegops* Eskov & Wunderlich, 1995 and described as *L.*? *cor* sp. nov. We confirm the existence of previously contentious numerous tarsal and metatarsal trichobothria on *Burlagonomegops alavensis* Penney, 2005, and reinterpret the mouthpart morphology of *Grandoculus chemahawinensis* Penney, 2004. In light of our new data, the family diagnosis for Lagonomegopidae is emended and the family Grandoculidae Penney, 2011 is synonymized with Lagonomegopidae.

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Introduction

The family Lagonomegopidae Eskov & Wunderlich, 1995 is a small group of spiders only known from inclusions in Cretaceous ambers. The family was placed within the superfamily Palpimanoidea primarily based on the presence of cheliceral peg teeth (Forster & Platnick 1984; Eskov & Wunderlich 1995). Lagonomegopids were named for the most diagnostic feature of the group: two large (*mega* in Greek) eyes (*-ops*) positioned on the anterolateral flanks (*lagono-*) of the carapace. This character is not found in any other fossil or extant spider family (Eskov & Wunderlich 1995; Jocqué & Dippenaar-Schoeman 2006). All fossils discovered to date (24 specimens) have been regarded as juveniles/females because of the absence of sexual differentiation in the male palp (note that Wunderlich 2008 reported a probable adult female but did not provide evidence for this assumption). Although potentially unremarkable and reflecting the hand of chance or a taphonomic bias towards preservation of juvenile specimens in amber (smaller organisms are more easily trapped in resin; see Martínez-Delclòs *et al*. 2004), another explanation is that these spiders had a female-biased sex ratio, perhaps a consequence of parthenogenetic events. Female-biased sex ratios have been noted in some social (see Avilés 1997) and solitary (Gunnarsson & Andersson 1996) extant spiders, and Wunderlich (2004) reported an unusual sex ratio for members of the Baltic archaeid *Eoarchaea*, with more than 30 females and no males discovered. Although describing new taxa using putatively juvenile specimens can be problematic, the lagonomegopids described herein possess diagnosably distinct characters sufficient to delineate their diversity.

Four genera have been recognized within the family: *Lagonomegops* Eskov & Wunderlich, 1995, *Grandoculus* Penney, 2004, *Burlagonomegops* Penney, 2005, and *Zarqagonomegops* Kaddumi, 2007. *Lagonomegops* contains two species: *L. sukatchevae* Eskov & Wunderlich, 1995, based on two specimens from Coniacian–Santonian Taymir (Yantardakh) amber, and *L. americanus* Penney, 2005, from Turonian New Jersey amber (see description in Penney 2002). The genus *Grandoculus* consists only of the type species *G. chemahawinensis* Penney, 2004 from Campanian Cedar Lake amber, which was recently transferred to a new family by Penney (2011) (see below). Two species have been described within *Burlagonomegops*: *B. eskovi* Penney, 2005, from late Albian Burmese amber, and *B. alavensis* Penney, 2006 from Albian Álava

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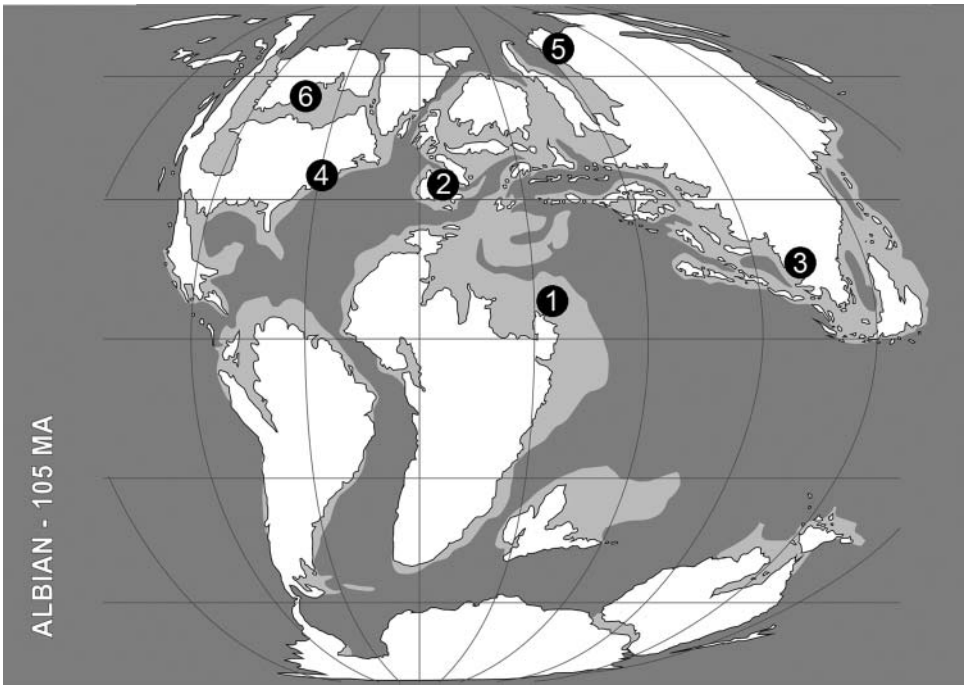

Figure 1. Cretaceous distribution of described Lagonomegopidae. The palaeogeographical map (redrawn from Blakey 2011) corresponds to the middle Albian (*c*. 105 Ma). (1) Jordan (Albian): *Zarqagonomegops wunderlichi*. (2) Spain (Albian): (2.1) Álava amber, Peñacerrada I (= Moraza) and II outcrops (Burgos and Álava, respectively): *Burlagonomegops alavensis*, *Lagonomegops*? *cor* sp. nov., *Spinomegops arcanus* sp. nov.; (2.2) San Just amber (Teruel): *Spinomegops aragonensis* sp. nov.; (2.3) El Soplao amber (Cantabria): *Soplaogonomegops unzuei* gen. et sp. nov. (3) Myanmar (late Albian): *Burlagonomegops eskovi*. (4) New Jersey, USA (Turonian): *Lagonomegops americanus*. (5) Yantardakh, Taimyr, Russia (Coniacian–Santonian): *Lagonomegops sukatchevae*. (6) Cedar Lake, Canada (Campanian): *Grandoculus chemahawinensis*.

amber. *Zarqagonomegops* Kaddumi, 2007 is represented by the type and only species: *Z. wunderlichi* from Albian Jordanian amber. The diagnostic characters for *Zarqagonomegops* are weak, however, and Wunderlich (2008) suggested that the genus might be congeneric with *Lagonomegops*. More recently, 12 specimens regarded as *Burlagonomegops* ?*eskovi* were recognized from Burmese amber (Wunderlich 2008).

The widespread distribution of lagonomegopids during the Cretaceous (Fig. 1) and their absence from well-known Tertiary resins suggest that the family met its demise in the Late Cretaceous, perhaps related to the end-Cretaceous mass extinction event (Penney 2005). Based on the short legs and large eyes, lagonomegopids have been regarded as free hunters (not constructing a web) (Eskov & Wunderlich 1995), a condition present in most, if not all, palpimanoids (Forster & Platnick 1984). Others have hypothesized that, due to overall similarity in habitus, lagonomegopids occupied the same ecological position as salticids (Eskov & Wunderlich 1995; Penney 2005), a diverse group of large-eyed, jumping spiders unknown from the Cretaceous (Dunlop *et al*. 2011), but this assertion remains conjectural at best.

Here we describe new lagonomegopids from Spanish Albian amber that significantly increase the diversity of the family and allow redefinition of its limits.

Geological setting

Two Cretaceous basins have yielded significant amber with bioinclusions in Spain: the Basque-Cantabrian Basin (northern Spain) and the Maestrat Basin (eastern Spain) (Delclòs *et al*. 2007). The amber deposits of the Maestrat Basin are associated with fluvial-swamp environments, and those of the Basque Cantabrian Basin are linked with deltaic-shore marine environments (see synthesis in Peñalver & Delclòs 2010).

The amber from the Peñacerrada I (= Moraza) outcrop belongs to the so-called Álava amber (Alonso *et al*. 2000), which is located in the eastern portion of the Basque Cantabrian Basin in Burgos Province. Three spiders have been described from Álava amber: the lagonomegopid *Burlagonomegops alavensis* Penney, 2006, an araneid, and an oonopid (Penney 2006; Penney & Ortuño 2006; Saupe *et al*. 2012). An additional spider was figured by Alonso *et al*. (2000, fig. 9.6). More than 2000 arthropod inclusions have been discovered from the outcrop, with Araneae comprising 2.4% of the diversity (Delclòs *et al*. 2007; Peñalver & Delclòs 2010).

The El Soplao outcrop is located in the north-western part of the Basque-Cantabrian Basin in Cantabria Autonomous Community, near the locality of Rábago (Najarro *et al*. 2009). The deposit is potentially the largest amber site with

bioinclusions in Spain (Najarro *et al*. 2010), and more than 500 arthropod inclusions have been obtained so far. Among spider fossils, only an oonopid has been formally described from this locality (Saupe *et al*. 2012), but the tarsal claws from an unidentified spider and spider silk were figured by Najarro *et al*. (2009, fig. 9E, F).

The San Just outcrop is located in the Oliete sub-basin within the Maestrat Basin in Teruel Province (Peñalver *et al*. 2007). Over 200 bioinclusions have been discovered to date, including a recently described oonopid (Saupe *et al*. 2012), a spider web with trapped prey (Peñalver *et al*. 2006), and a figured spider (Delclòs *et al*. 2007, fig. 3F).

Geological and palynological studies indicate an Albian age for all these deposits (Alonso *et al*. 2000; Barrón *et al*. 2009; Najarro *et al*. 2009, 2010; Villanueva-Amadoz *et al*. 2010).

Material and methods

All amber pieces were cut, polished, and embedded in epoxy resin prior to receipt by the authors. Drawings of the specimens were made under incident and transmitted light with the aid of a camera lucida attached to a Leica DM2500 M microscope. Drawings were then inked and scanned into Adobe Photoshop CS4. Photographs were taken with a Canon EOS 5D Mark II camera attached to a Leica M205 C stereomicroscope and a Leica DM2500 M microscope. Image stacks were merged using Helicon Focus 4.2.1 software (HeliconSoft, Ukraine). All measurements were taken with an ocular graticule.

Eye homology follows Eskov & Wunderlich (1995). 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). Larger fractions indicate more distally placed structures (e.g. a trichobothrium at one-third of tibial length is more proximal than one at two-thirds of tibial length). Trichobothria are marked with asterisks (*) in drawings and photographs.

Anatomical abbreviations

ALE: anterior lateral eye(s); ALS: anterior lateral spinneret(s); AME: anterior median eye(s); cx: coxa(e); fe: femur/-ora; MS: median spinneret(s); mt: metatarsus/-i; PLE: posterior lateral eye(s); PLS: posterior lateral spinneret(s); PME: posterior median eye(s); pt: patella(e); ti: tibia(e); tr: trochanter(s); ts: tarsus/-i.

Institutional/collection abbreviations

CES: Colección El Soplao (Spain); **CPT**: Colección Paleontológica de Teruel (Spain); **MCNA**: Museo de Ciencias Naturales de Álava (Spain); **MCZ**: Museum of Comparative Zoology at Harvard University, Cambridge, MA (USA); **PIN**: Paleontological Institute of the Russian Academy of Sciences, Moscow (Russia).

Additionally examined samples

(1) *Burlagonomegops alavensis* Penney, 2006, holotype; Álava amber (Peñacerrada II outcrop), Álava, Spain. Deposited at the MCNA. Images of this sample were taken with a Leica DFC280 camera attached to a Leica M420 stereomicroscope and a Nikon Labophot2-Pol microscope.
(2) *Grandoculus chemahawinensis* Penney, 2004, holotype; Cedar Lake amber, Manitoba, Canada. Deposited at the MCZ.

Trichobothria determination

The trichobothrial pattern in Lagonomegopidae has been granted taxonomic significance (cf. *Burlagonomegops*) but is often difficult to assess and has been embroiled in controversy. Accordingly, we point out the criteria employed for recognizing trichobothria in the studied lagonomegopids and for differentiating them from regular leg and tactile setae. Tactile setae are short, thin, erect hairs that act as sensory structures (mechanoreceptors) (Foelix 2011). They are usually found in lagonomegopids on distal podomeres, at least ventrally and dorsally. We acknowledge that some of the tactile setae recognized in the specimens described here could correspond to taste hairs (chemoreceptors) *sensu* Foelix (2011, fig. 4.15).

Four main criteria were followed, with three subsidiary guides depending on the circumstance: (1) trichobothria are thinner than regular leg setae and tactile setae; (2) trichobothria have a constant thickness, whereas regular leg setae and tactile setae taper towards their tip; (3) trichobothria, although variable in length, tend to be longer than regular leg setae and much longer than tactile setae; and (4) whereas trichobothria emerge from the dorsal part of the podomere, regular leg setae arise from all podomere positions; the same logic follows for tactile setae, which can be present ventrally. Subsidiary criteria are: (1) the bothrium (i.e. the often-ridged, dome-like organ from which the trich emerges) is sometimes conspicuous; however, tactile setae can arise from a relatively well-developed socket (Foelix 2011, fig. 4.1), and shrivelling can cause the base of regular leg setae to appear dome-like; (2) trichobothria are usually erect (i.e. emerge orthogonal to the leg podomere), whereas regular leg setae are adpressed to the podomere cuticle, and tactile setae are more obliquely disposed to the podomere surface; (3) trichobothria typically exhibit the flexible, sinuous structure present in life, whereas regular leg setae and tactile setae tend to be stiff. Nevertheless, some tactile setae can be slightly sinuous and, depending on the biostratinomic processes (e.g. the spider's last movements in resin), trichobothria can appear stiff.

Even following these criteria, the determination of trichobothria is often a challenge and, in a few cases, it was difficult to ascertain whether a hair-like structure corresponds to a trichobothrium or a tactile seta. We note that the total absence of trichobothria reported from *Zarqagonomegops wunderlichi* is surprising and should be reassessed.

Systematic palaeontology

Order **Araneae** Clerck, 1757
Family **Lagonomegopidae** Eskov & Wunderlich, 1995

Type species. *Lagonomegops sukatchevae* Eskov & Wunderlich, 1995.

Emended diagnosis. Minute to small spiders (1 to nearly 5 mm). Cheliceral foramen absent. Chelicerae bearing several pointed, relatively short peg teeth (up to five) on the unguis. Carapace with two anterolateral protrusions, where a pair of large eyes (tentatively interpreted as the PME) are placed. Endites subtriangular, directed across the labium, almost meeting at the midline, with serrula as a single row of teeth. Labium subtriangular, wider than long. Sternum shield-like, without marginal projections between or at the middle of coxae. Six spinnerets. Several tibial trichobothria present, with the subdistal metatarsal trichobothria longest. Three tarsal claws, unpaired claw hook-like. Female palpal tarsi lacking a claw.

Remarks. Some characters show a wider variability within the current framework of Lagonomegopidae or have been impossible to assess from all species. Although they have not been included in the family diagnosis, other characters worthy of consideration are: carapace and chelicerae shape; number of eyes; presence of cuticular specializations on legs 1 + 2; presence of femoral spines; and further features associated with trichobothrial pattern. Among them, the number of eyes and the trichobothrial pattern are often difficult to discern in the specimens and can be easily overlooked in the descriptions.

Carapace shape ranges from compact to elongated, with varying degrees of elevation. The carapace can also have a distinct cephalic region, which can be projected forward, and the cephalic region, if distinct, can be constricted to different degrees, even forming a neck. Furthermore, the area of cheliceral insertion and mouthparts can be separated in the vertical plane (i.e. chelicerae can be inserted at an elevated point of the carapace).

Chelicerae range from almost straight to gently or strongly procurved, and their relative size (not only length) is variable.

Up to three additional pairs of smaller eyes may be present: up to two pairs (tentatively interpreted as the AME and ALE) below and slightly anterior to the large PME, and one pair (tentatively interpreted as the PLE) placed at the posterior margin of the anterolateral protrusions of the carapace.

Cuticular modifications on legs 1 + 2 can be present, composed of hairs forming scopulae (densely packed) or bristles hair- to spine-like in thickness and not forming scopulae (loosely arranged).

Erect, curved spines on distalmost femora, variable in thickness, are present frequently.

Apart from the trichobothrial characters delimited in the diagnosis, (1) the tibial trichobothria can be arranged in pairs; (2) additional, shorter metatarsal trichobothria can be present in a more proximal position; and (3) tarsal trichobothria can be present.

Genus ***Lagonomegops*** Eskov & Wunderlich, 1995

Type species. *Lagonomegops sukatchevae* Eskov & Wunderlich, 1995 (holotype PIN 3311/564; paratype PIN 3311/573; the current location of this material is unknown (Penney 2005; Rasnitsyn & Eskov pers. comm. 2012)).

Occurrence. Early to Late Cretaceous (Albian to Coniacian–Santonian). *Lagonomegops americanus* Penney, 2005, from Turonian New Jersey amber; *L. sukatchevae* Eskov & Wunderlich, 1995, from Coniacian–Santonian Yantardakh amber, Taimyr.

Lagonomegops*? *cor sp. nov.
(Figs 2, 3)

Diagnosis. Carapace almost as long as high (ratio prosomal length/height close to 1), with maximum height reached anteriorly; heart-shaped when viewed from above, resulting from greatest carapace width reached anteriorly and the conspicuous frontal protrusions that create a pronounced, acute frontal depression. Tarsi not longer than metatarsi.

Derivation of name. The specific epithet is the Latin term *cor*, meaning heart, and is treated as a noun in apposition (hence in nominative case). The name refers to the heart-shaped outline (in abstraction) of the carapace when viewed from above.

Material. MCNA-13295, juvenile or adult female from Álava amber, Peñacerrada I (= Moraza) outcrop (Burgos, Spain). The cuticle is clear, especially in the proximal part of all legs, almost to the point of invisibility. Remains of cuticle cut diagonally through the prosoma. The opisthosoma is lifted above the prosoma, with the distal portion not preserved. Most of leg 2 is missing. A bubble occurs inside the left PME, and several others are present inside some leg segments. The specimen is preserved together with a fragmentary long leg of an undetermined arthropod and organic debris.

Description. Body length not measurable but >1 mm long (Fig. 2A). Carapace compact, heart-shaped when viewed from above (Fig. 2B); very raised, with all

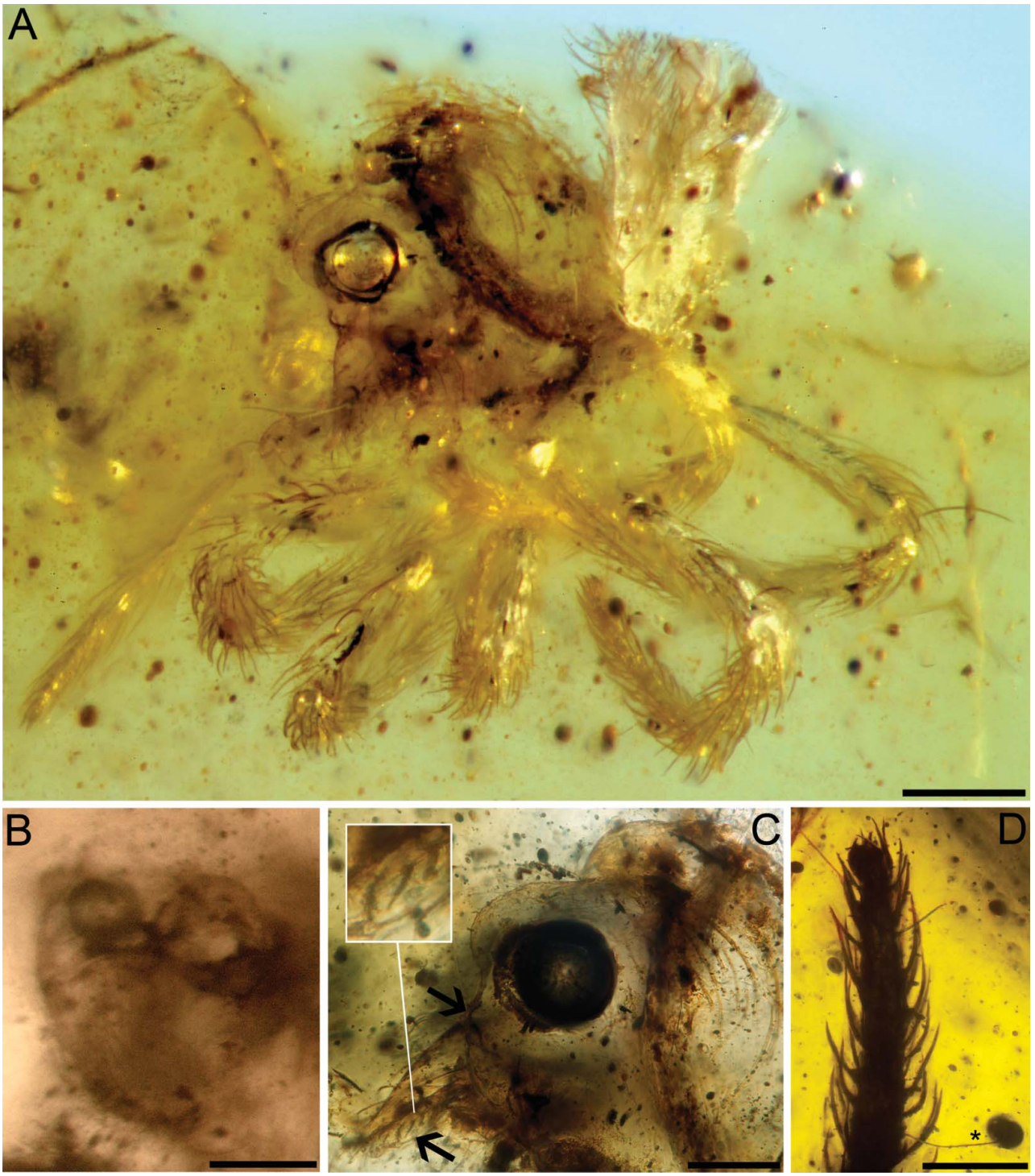

Figure 2. *Lagonomegops*? *cor* sp. nov., MCNA-13295; **A,** lateral habitus; **B,** dorsal view of the carapace; **C,** lateral view of the carapace; note the ALE/AME? (upper arrow) and cheliceral peg teeth (lower arrow), magnified in the detailed image; **D,** left mt and ts 4; note the elongated trichobothrium on distal mt and a tactile seta on distal ts. Scale bars: A, B = 0.2 mm; C, D = 0.1 mm.

sides steeply sloping but a more gradual slope towards posterior border; 0.52 mm long, 0.43 mm wide at widest point at about anterior third, 0.50 mm high. Cephalic region of carapace not distinct (anterior part of carapace not constricted or projected forward; no suture delimiting the cephalic region from the thoracic region of the carapace). Anterolateral protrusions of the carapace large, >0.20 mm in diameter, occupying more than

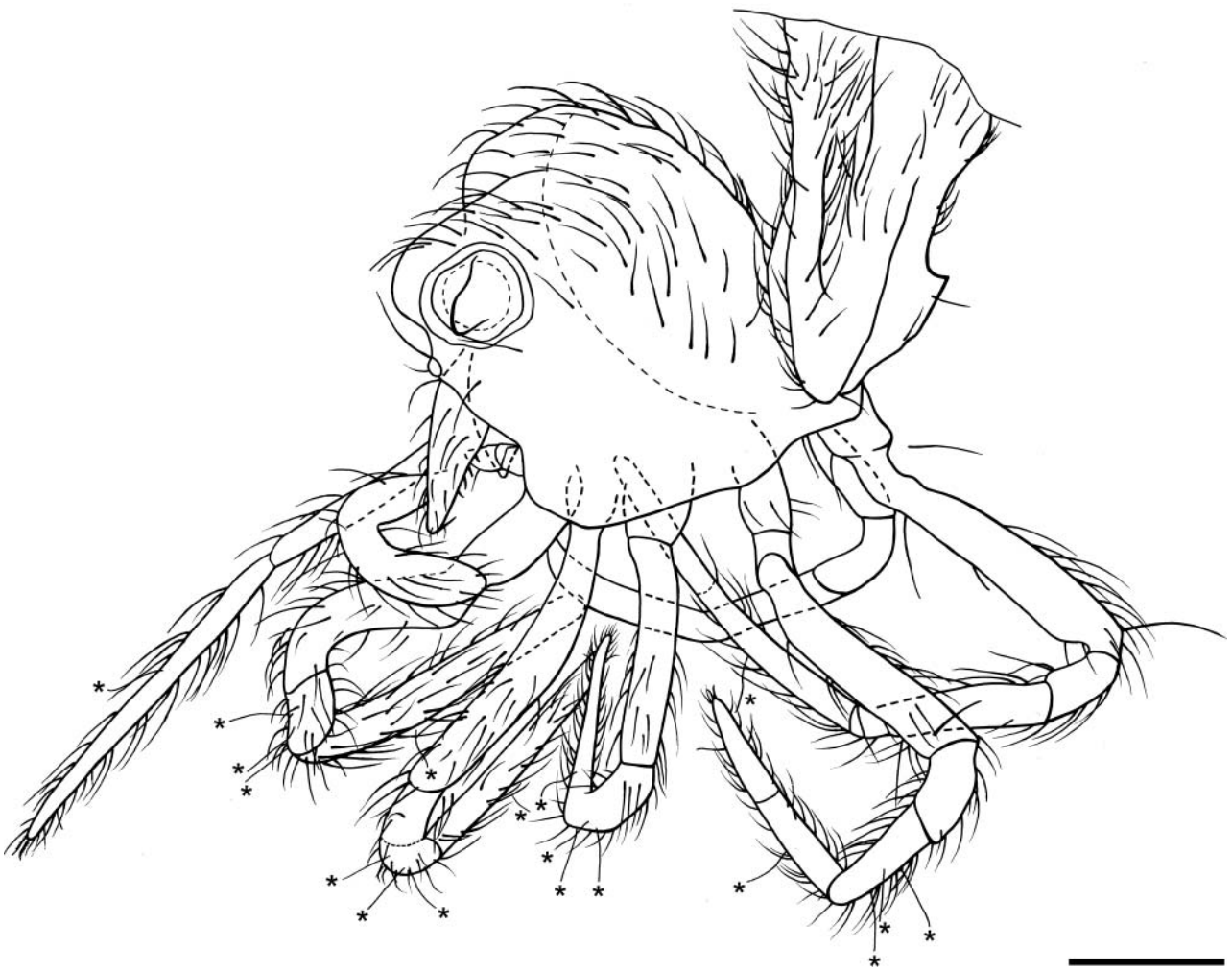

Figure 3. Camera lucida drawing of *Lagonomegops*? *cor* sp. nov. in lateral habitus, MCNA-13295; right leg 2 and setation of right leg 3 have been omitted to improve visibility. Scale bar = 0.2 mm.

one-third of carapace length; frontal invagination created by the anterolateral protrusions very pronounced and acute (not rounded) (Fig. 2B, C), 0.11 mm long, 0.22 mm wide. Fovea absent. Carapace clothed in anteriorly directed, plumose setae, 0.09−0.11 mm long. Chelicerae subconical, gently procurved, anteriorly directed; 0.27 mm long, 0.12 mm broad at base; cheliceral insertion distinctly separated from the mouthparts in the vertical plane (i.e. chelicerae inserted at an elevated point of the carapace). Fang not visible. Ental margin of cheliceral unguis with four pointed, rather short peg teeth, 0.02 mm long (Fig. 2C). Cheliceral stridulatory files not visible or absent. Chelicerae covered with plumose setae, up to 0.08 mm long. Four eyes visible. PME 0.12 mm in diameter, situated on the anterolateral protrusions of the carapace, very faintly anteriorly directed if not completely laterally directed; strongly sclerotized ring around PME visible. ALE (AME?) around 3× smaller than PME, 0.04 mm in diameter, situated below the distal half of the PME, separated from the PME by slightly more than their diameter, close to the clypeal margin (Fig. 2C). Labium not visible. Endites elongated, subtriangular; serrula present. Sternum shape not discernible, but convex without tubercles and with plumose setae. Opisthosoma shrivelled, not measurable; not sclerotized; covered in plumose setae, 0.08−0.10 mm long. Spinnerets not preserved.

Legs relatively short and stout, no legs enlarged. Ts as long as mt or slightly shorter. Leg formula 4123/4213: leg 1 fe 0.34 mm, pt *c*. 0.11 mm, ti 0.25 mm, mt 0.23 mm, ts 0.23 mm, total *c*.1.16 mm; leg 2 fe 0.33 mm, pt 0.11 mm, ti unknown, mt 0.20 mm, ts 0.20 mm, total >0.84 mm (ti lacking); leg 3 fe 0.30 mm, pt 0.11 mm, ti 0.16 mm, mt 0.16 mm, ts 0.14 mm, total 0.87 mm; leg 4 fe 0.36 mm, pt 0.13 mm, ti 0.29 mm, mt 0.27 mm, ts 0.23 mm, total 1.28 mm. Three tarsal claws; paired claws 0.04 mm long, with six/seven teeth; median claw hook-like; onychium

absent. Absence of setal scopulae or bristle-based, non-scopular structures on ts or mt 1 + 2. Legs covered in strong plumose setae, 0.08−0.10 mm long. Faint (almost hair-like in thickness), erect, curved, plumose, elongated bristle present on at least distal fe 1 + 3 + 4; 0.13−0.18 mm long. Tarsal trichobothria absent. Trichobothria dorsally on all ti and mt as follows: (1) Three on ti, two paired at two-thirds of its length and one at nine-tenths of its length, relatively elongated, 0.06−0.08 mm long; and (2) one at seven-tenths of mt, elongated to very elongated, 0.08−0.12 mm long (Fig. 2D). Tactile setae dorsally and ventrally on all mt and ts as follows: (1) one dorsally on distal mt, 0.06 mm long; (2) one to three dorsally on distal ts (Fig. 2D), *c.* 0.05 mm long; and (3) up to three ventrally on distal ts, very short, 0.03 mm long.

Palpus slender; fe *c*. 0.17 mm long, pt + ti 0.16 mm long, ts 0.18 mm long; bristles absent; with a long trichobothrium distally on palpal ti at two-thirds of its length, 0.11 mm long. Palpal claw absent. Plumose setae present, 0.08 mm long.

Remarks. The genus *Lagonomegops* is weakly delimited because the diagnosis is based on the absence of potentially apomorphic features present in other genera of Lagonomegopidae. Thus, *Lagonomegops* would clearly benefit from taxonomic revision if more data become available and clearer insight is gained into the phylogenetic relationships among taxa. With that said, MCNA-13295 is tentatively assigned to the genus *Lagonomegops* based on: (1) the absence of a distinctly raised cephalic region that projects forward as present in *Burlagonomegops* and *Soplaogonomegops* gen. nov.; (2) the lack of tarsal trichobothria (present in *Burlagonomegops* and *Spinomegops aragonensis* sp. nov.); and (3) the absence of cuticular specializations on the first two pair of mt and ts, i.e. the scopulae of densely arranged setae present in *Grandoculus* and the non-scopular bristles diagnostic of *Spinomegops* gen. nov.

Lagonomegops? *cor* sp. nov. differs from previously described species of *Lagonomegops* in possessing a carapace almost as long as high (length/height ratio close to 1; other *Lagonomegops* have carapaces not as high and distinctively longer). For example, the holotype of *L. sukatchevae* has a prosomal length/height ratio of 1.57, while the paratype has a ratio of 2.10 (Eskov & Wunderlich 1995). *L. americanus* has a similar prosomal length/height ratio of 1.92. Moreover, the maximum height of the carapace is reached anteriorly in *L.*? *cor*, but it is reached posteriorly in *L. sukatchevae* (Eskov & Wunderlich 1995, figs 3, 4). The anterolateral protrusions of the carapace are very prominent in *L.*? *cor* when compared to known lagonomegopid diversity, even more pronounced than *Grandoculus chemahawinensis* (Penney 2004, fig. 1A). On the contrary, the anterolateral protrusions are faint in *L. sukatchevae* and *L. americanus* (Eskov & Wunderlich 1995, fig. 1; Penney 2002, pl. 1.2). Finally, the ts are distinctly longer than the mt in *L. sukatchevae* (Eskov & Wunderlich 1995, fig. 7; Wunderlich 2008) but shorter or subequal in length in *L. americanus* (see measurements in Penney 2002) and the new species.

Genus ***Spinomegops*** gen. nov.

Type species. *Spinomegops arcanus* sp. nov.

Other species included. *Spinomegops aragonensis* sp. nov.

Diagnosis. Presence of numerous non-scopular (i.e. sparse, not arranged in dense rows), erect (almost perpendicular to the podomere), elongated (longer than regular leg setae), laterally disposed (both prolaterally and retrolaterally, not dorsally or ventrally), non-plumose bristles on distal metatarsi and tarsi of legs 1 + 2. Bristle thickness spine-like (*S. arcanus*) or almost hair-like (*S. aragonensis*).

Derivation of name. The epithet is the combination of *spina*, spine in Latin, after the diagnostic feature of the genus, and *Lagonomegops*, type genus of the family. The name is masculine.

Spinomegops arcanus sp. nov.
(Figs 4, 5)

Diagnosis. Carapace compact (not elongated), with maximum height reached posteriorly. Tarsal and metatarsal non-scopular bristles spine-like in thickness. Tibial trichobothrial pattern as follows: a single one at two-thirds of tibial length and another one subdistally, paired at least on legs 3 + 4. Spines on palpal tibiae and palpal tarsi present.

Derivation of name. From the Latin adjective *arcanus* meaning hidden, secret or mysterious, referring to the inconspicuous shape of the specimen resulting from the cleared cuticle.

Material. MCNA-13307, juvenile or adult female from Álava amber, Peñacerrada I (= Moraza) outcrop, Burgos, Spain. The cuticle is cleared. The prosoma is distorted, and right legs 1 and 2 are badly preserved beyond the ti. Large bubbles are present inside the prosoma and opisthosoma, and additional ones occur inside the left PME and some leg segments. The spider is surrounded by organic debris.

Description. Body *c.*1.07 mm long (Fig. 4A). Carapace compact, oval when viewed from above; very raised, with lateral sides steeply sloping, posterior slope most likely steeply sloping; *c*. 0.53 mm long, *c*. 0.40 mm wide, *c*. 0.30 mm high (measurements approximate due to carapace distortion). Cephalic region of carapace not distinct (anterior part of carapace not constricted or projected forward; no suture delimiting the cephalic region from the thoracic region of the carapace). Anterolateral protrusions of the carapace apparently small, diameter not measurable; frontal depression created by the anterolateral protrusions slightly pronounced and rounded (not acute); 0.03 mm long,

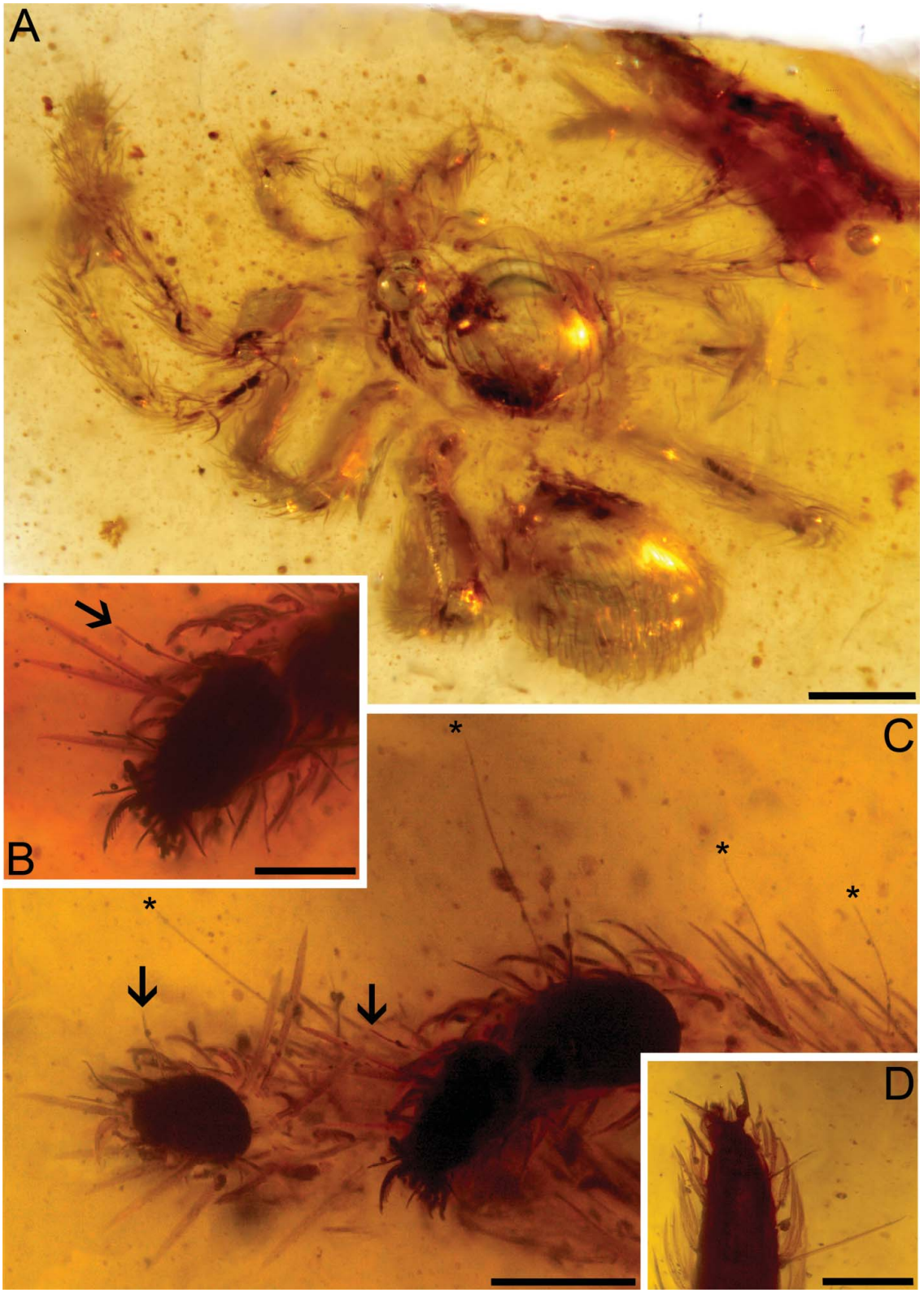

Figure 4. *Spinomegops arcanus* sp. nov., MCNA-13307; **A,** dorsal habitus; **B,** left ts 2 showing three retrolaterally disposed spine-like bristles and dorsal and ventral tactile setae; note the proximal hair-like structure tentatively interpreted as a tactile seta (arrow); **C,** distal podomeres of left legs 1 + 2, showing pro- and retrolaterally disposed spine-like bristles, tactile setae, and trichobothria; note the hair-like structures proximally on ts, tentatively interpreted as tactile setae (arrows); **D,** left ts 3; note the isolated proximal bristle and the more distal tactile seta. Scale bars: A = 0.2 mm; B, D = 0.05 mm; C = 0.1 mm.

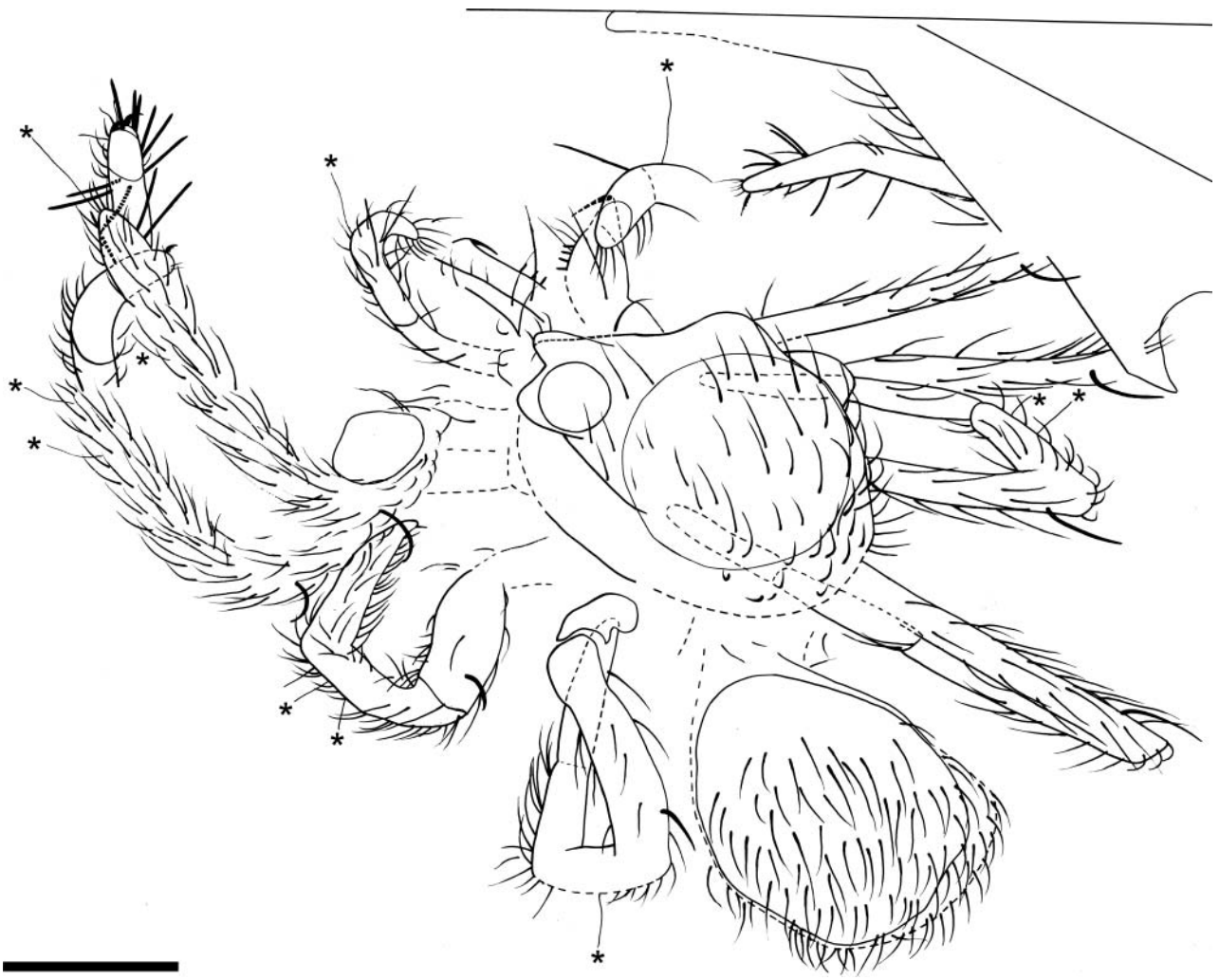

Figure 5. Camera lucida drawing of *Spinomegops arcanus* sp. nov. in dorsal habitus, MCNA-13307. Scale bar = 0.2 mm.

0.25 mm wide. Fovea absent. Carapace clothed in anteriorly directed, plumose setae, *c*. 0.05 mm long. Chelicerae subconical, anteriorly directed; 0.18 mm long, 0.08 mm broad at base; cheliceral insertion not discernible. Fang not visible. Ental margin of cheliceral unguis with four visible pointed peg teeth, 0.03−0.04 mm long. Single, erect, particularly elongated setae dorsoproximally on chelicerae, 0.14 mm long. Cheliceral stridulatory files not visible or absent. Chelicerae covered with plumose setae, up to 0.05 mm long. Only the PME visible, 0.14 mm in diameter; situated posterior to the anterolateral protrusions of the carapace; strongly sclerotized ring around PME present. Labium likely subtriangular, not measurable. Endites elongated, subtriangular, converging and almost meeting at the midline; 0.09 mm long, 0.08 mm wide at base, 0.03 mm wide at tip; serrula well developed, with a single row of teeth present that decreases in length distally. Sternum shield-shaped, convex; *c*. 0.40 mm long, *c*. 0.35 mm wide; marginal projections absent; without tubercles; covered in finely plumose setae. Opisthosoma ovoid, laterally compacted; 0.50 mm long, 0.20−0.30 mm wide, *c*. 0.40 high; clothed in plumose setae, 0.08 mm long. ALS and PLS well developed; ALS ellipsoidal in section, 0.10 mm long, 0.12 mm wide, 0.07 mm high, separated by 0.05 mm; PLS subcircular in section, 0.09 mm long, 0.06 mm wide, separated by 0.13 mm. PMS not visible. Anal tubercle rhomboid in shape; *c*. 0.04 mm long, 0.06 mm wide; covered in short, plumose setae, 0.04 mm long.

Legs relatively short and rather stout, no legs enlarged. Leg formula 2143/1243: leg 1 fe 0.37 mm, pt + ti + mt 0.60 mm, ts 0.23 mm, total 1.20 mm; leg 2 fe 0.42 mm, pt + ti + mt 0.57 mm, ts 0.20 mm, total 1.19 mm; leg 3 fe 0.31 mm, pt 0.05 mm, ti 0.19 mm, mt 0.19 mm, ts 0.19 mm, total 0.93 mm; leg 4 fe 0.40 mm, pt 0.06 mm, ti 0.23 mm, mt 0.23 mm, ts 0.19 mm, total 1.11 mm. Three tarsal claws; paired claws 0.03 mm long, with seven/eight

teeth; median claw hook-like; onychium absent. Presence of numerous bristles on mt and ts 1 + 2, sparsely disposed (not forming scopulae), strong, i.e. clearly spine-like, in lateral position (both prolaterally and retrolaterally, not dorsally or ventrally), smooth (not plumose as the leg setation), subperpendicular regarding the ts; 0.08−0.12 mm long (Fig. 4B−D). Visible bristles are arranged as follows (bristles on right leg not detailed due to bad preservation, though clearly present): (1) left leg 1: two at the tarsal–metatarsal articulation, nine on ts apparently at two distinct points (two and two entally, two and three ectally); (2) left leg 2: five on ts. Bristles absent from ts or mt 3 + 4, except for a single one visible on ts 3 (Fig. 4D). Legs covered in plumose setae; 0.07−0.09 mm long. Erect, curved, plumose bristle present on all distal fe; *c*. 0.12 mm long. Tarsal trichobothria considered absent (see discussion). Trichobothria dorsally on all ti and mt as follows: (1) two on ti, 0.06−0.09 mm long: one at two-thirds of its length and one at nine-tenths of its length (although, at least on legs 3 + 4, two paired trichobothria may exist at nine-tenths of ti length); and (2) one at four-fifths of mt, very elongated, 0.16 mm long, shorter on legs 3 + 4 (Fig. 4C). Tactile setae dorsally and ventrally on all mt and ts as follows (Fig. 4B−D): (1) one/two dorsally on distal mt, 0.05 mm long; (2) one dorsally at about one-half of ts 1 + 2, relatively elongated, 0.06 mm long; (3) up to four dorsally on distal ts (single on legs 3 + 4), 0.04 mm long; (4) a few ventrally on distal mt, relatively elongated, 0.06 mm long; and (5) up to four ventrally along all ts length, 0.04−0.05 mm long.

Palpus slender; fe 0.15 mm long, pt 0.08 mm long, ti *c*. 0.13 mm long, ts 0.14 mm long; ti bearing at least two long, stiff, prolateral spines, one at about one-half of ti and one at about one-quarter of ts, 0.13 mm long; with a long trichobothrium on one-quarter of ti, 0.11 mm long. Palpal claw absent. Plumose setae present, 0.07 mm long.

Spinomegops aragonensis sp. nov.
(Figs 6, 7)

Diagnosis. Carapace elongated, with maximum height reached anteriorly. Eight eyes present. Tarsal and metatarsal non-scopular bristles almost hair-like in thickness. Tibiae with at least two short, paired trichobothria proximal to mid-length, and two longer trichobothria distal to mid-length. Single tarsal trichobothrium present. Spines on palpal tibiae and palpal tarsi absent.

Derivation of name. After Aragón, the Spanish autonomous community where the San Just outcrop is located.

Material. CPT-4155, juvenile or adult female from San Just amber, Teruel, Spain. The cuticle is cleared, which revealed characters that tend to be hidden, like the eyes and trichobothria. The distal portion of the opisthosoma and distal podomeres of leg 4 are not preserved. A large bubble is present inside the prosoma, and additional ones are present within some leg segments.

Description. Body 1.73 mm long as preserved (Fig. 6A). Carapace elongated, subpiriform when viewed from above; raised, with lateral sides steeply sloping and posterior sides moderately sloping (Fig. 6B); 1.02 mm long, 0.56 mm wide at widest point, *c*. 0.55 mm high. Cephalic region of carapace distinct, projected forward, corresponding mostly to the anterolateral protrusions projected *c*. 0.20 mm beyond the chelicerae insertion (Fig. 6B). Cephalic region not constricted, 0.43 mm wide distally, with two expanded, relatively narrow, anterolateral protrusions, *c*. 0.35 mm in diameter; frontal depression created by the anterolateral protrusions pronounced and rounded (not acute), 0.06 mm long, 0.26 mm wide. No suture delimiting the cephalic region from the thoracic region of the carapace. Fovea absent. Carapace clothed in anteriorly directed, plumose setae, 0.10−0.12 mm long. Chelicerae subconical, procurved, slightly anteriorly directed (Fig. 6B); *c*. 0.40 mm long, 0.20 mm broad at base; cheliceral insertion distinctly separated from the mouthparts in the vertical plane (chelicerae inserted at an elevated point of the carapace). Fang relatively stout, not measurable. Peg teeth not visible. Single, erect, particularly elongated setae dorsoproximally on chelicerae (Fig. 6B), 0.15 mm long. Cheliceral stridulatory files not visible or absent. Chelicerae covered with setae, not conspicuously plumose at least distally, 0.05 mm long. Eight eyes present. PME large (Fig. 6C, D), 0.16 mm in diameter; situated on the anterolateral protrusions of the carapace, slightly anteriorly directed; strongly sclerotized ring around PME visible. AME, ALE, and PLE 4× smaller than PME, 0.04 mm in diameter. AME and ALE contiguous, AME placed below ALE, with both situated below the distal half of the PME, close to the clypeal margin (Fig. 6C). PLE placed at the posterior margin of the anterolateral protrusions of carapace (Fig. 6D), separated 0.25 mm from the PME centre. Labium not visible. Endites elongated, subtriangular, converging and likely almost meeting at the midline; not measurable; serrula well developed, with a single row of at least 24 teeth. Sternum shield-shaped, relatively small, convex; *c*. 0.43 mm long, 0.30 mm wide at widest point anteriorly, at about three-fifths of its length; marginal projections absent; distal end between cx 4 rounded. Opisthosoma ovoid, not sclerotized; 0.65 mm long as preserved, 0.58 mm wide, 0.55 mm high; clothed in very faintly plumose setae, 0.10−0.12 mm long. Spinnerets not preserved.

Legs relatively short and stout, no legs enlarged. Ts as long as mt or slightly shorter. Leg formula 2143: leg 1 cx + tr 0.21 mm, fe 0.59 mm, pt 0.26 mm, ti 0.34 mm, mt 0.37 mm, ts 0.31 mm, total 2.08 mm; leg 2 cx + tr 0.26 mm, fe 0.63 mm, pt 0.23 mm, ti 0.39 mm, mt 0.33 mm, ts 0.33 mm, total 2.17 mm; leg 3 cx + tr 0.20 mm, fe 0.49 mm, pt 0.15 mm, ti 0.28 mm, mt + ts 0.44 mm, total 1.56 mm;

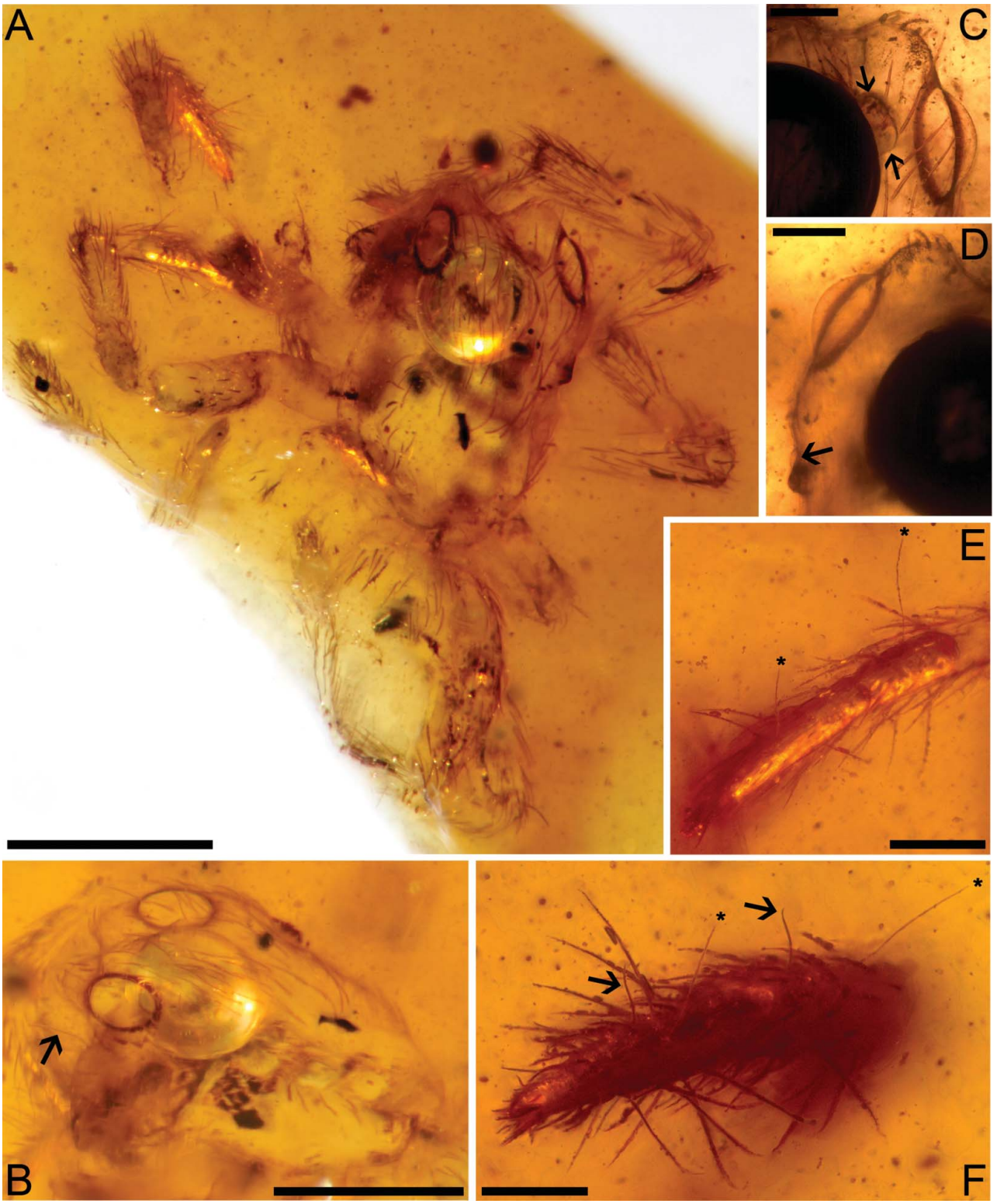

Figure 6. *Spinomegops aragonensis* sp. nov., CPT-4155; **A,** dorsal habitus; **B,** lateral oblique view of the carapace, showing the enlarged seta emerging from the dorsoproximal part of left chelicera (arrow); **C,** dorsal view of the right anterolateral protrusion of the carapace; note the AME (upper arrow) and the ALE (lower arrow) viewed through the cuticle; **D,** ventral view of the right anterolateral protrusion of the carapace, note the PLE (arrow); **E,** left mt and ts 2 showing some pro- and retrolaterally disposed bristles and trichobothria; **F,** left mt and ts 1 showing numerous pro- and retrolaterally disposed bristles, tactile setae (arrows), and trichobothria. Scale bars: A, B = 0.5 mm; C–F = 0.1 mm.

Figure 7. Camera lucida drawing of *Spinomegops aragonensis* sp. nov. in dorsal habitus, CPT-4155. The eyes have been tagged in the bottom left inset (setation omitted for clarity). Scale bar = 0.5 mm.

leg 4 cx + tr 0.19 mm, fe 0.55 mm, pt 0.20 mm, ti 0.34 mm, mt + ts 0.56 mm, total 1.84 mm. Three tarsal claws; paired claws 0.04 mm long, with 7–8 visible teeth; median claw hook-like; onychium absent. Presence of numerous bristles on mt and ts 1 + 2, sparsely disposed (not forming scopulae), faint (not as strong as in MCNA-13307), in lateral position (both prolaterally and retrolaterally, not dorsally or ventrally), smooth (not plumose as the leg setation), subperpendicular regarding the ts (Fig. 6E, F); 0.13–0.15 mm long. Visible bristles are arranged as follows: (1) right leg 1: one distally on mt and four on ts; (2) left leg 1: one on mt and *c.*10 on ts, starting beyond one-third of its length; (3) right leg 2: four distal on mt and *c*. 10 on ts, starting beyond one-third of its length; (4) left leg 2: two on mt and three on ts, starting beyond one-third of its length. Bristles absent from ts or mt 3 + 4. Legs covered in weakly plumose setae, only clearly evident on fe; 0.11–0.13 mm long. Erect, curved, finely plumose bristle present on all distal fe; 0.09 mm long. Tarsal trichobothria present (Fig. 6E, F). Trichobothria dorsally on all ti, mt and ts as follows: (1) five on ti: two paired at about one-third of its length, very short, 0.04 mm long; two paired at about two-thirds of its length, 0.10 mm long; and one dubious distal one, 0.06 mm long; (2) one at about four-fifths of mt, very elongated, *c*. 0.17 mm long; and (3) one placed slightly beyond ts mid-length, 0.10 mm long. Tactile setae dorsally and ventrally, at least, on mt and ts as follows (Fig. 6F): (1) one dorsally on distal mt, 0.06 mm long; (2) one dorsally slightly beyond one-half of ts, 0.06 mm long; and (3) a few ventrally along all ts length, *c*. 0.03 mm long.

Palpus slender; fe 0.24 mm long, pt + ti + ts 0.45 mm long; with a thin, erect, slightly curved bristle-like setae dorsodistally on fe, 0.11 mm long; with a long trichobothrium on 7–8/10 of ti, 0.14 mm long, and an additional pair of shorter trichobothria, 0.07 mm and 0.05 mm long respectively. Palpal claw absent. Plumose setae present, 0.10 mm long.

Remarks. The new genus *Spinomegops* is diagnosed by the distinctive non-scopular structure composed of bristles present on mt and ts 1 + 2. We group MCNA-13307 and CPT-4155 within a new genus based on this character taking into account: (1) the taxonomic significance that has been granted to cuticular specializations on distal podomeres of the first two pairs of legs in Lagonomegopidae (i.e. the dense setal scopulae present prolaterally in *Grandoculus chemahawinensis* (Penney 2004, 2011; see Discussion)), and Palpimanoidea (i.e. spatulate setae forming scopulae or not (Forster & Platnick 1984)), and (2) the morphological singularity of the described tarsal and metatarsal bristles found in MCNA-13307 and CPT-4155. Indeed, laterally placed (both prolaterally and retrolaterally) sparse bristles have not to our knowledge been described from any other known lagonomegopid or reported from any palpimanoid. These bristles are clearly stouter in *S. arcanus* sp. nov. than in *S. aragonensis* sp. nov. We recognize that our diagnosis lacks phylogenetic backing, but performing such analyses on lagonomegopids is difficult at present, considering outgroup choice is enigmatic at best, preservation of known diversity is often poor, and adults (at least males) are lacking. As such, our new genus and attendant diagnosis remains a hypothesis that can be overturned pending new analyses or data.

The existence of eight eyes in *S. aragonensis* confirms the presence of this character in the family, previously only reported as dubious from *Lagonomegops sukatchevae* (Eskov & Wunderlich 1995).

We assert that *S. arcanus* lacks tarsal trichobothria. However, even after applying the criteria used for discriminating between trichobothria and sensory or regular leg setae (see Trichobothria determination section), we found it challenging to discern the nature of the most proximal hair-like structure present dorsally on ts 1 + 2 (arrows in Fig. 4B, C). Tactile setae, which resemble in length and shape this hair-like structure, are also present ventrally on the distal mt and ts (Fig. 4C), and as such we consider the hair-like structure a tactile seta. This means, however, that within the same genus, one species has tarsal trichobothria whereas the other species lacks them. We acknowledge that this discrepancy may be problematical, since the presence of tarsal trichobothria is currently the primary diagnostic character for the genus *Burlagonomegops*.

Genus ***Soplaogonomegops*** gen. nov.

Type species. *Soplaogonomegops unzuei* gen. et sp. nov.

Diagnosis. Cephalic region constricted in a neck that projects forward; chelicerae inserted at an elevated point of the carapace, clearly separated from the mouthparts in the vertical plane. Neck base with a semicircular suture. Cuticular specializations on metatarsi/tarsi absent. Tarsal trichobothria absent.

Derivation of name. After the combination of El Soplao, the outcrop where the specimen was discovered, and *Lagonomegops*, type genus of the family. The name is masculine.

Soplaogonomegops unzuei sp. nov.
(Figs 8, 9)

Diagnosis. As for the genus (see above).

Derivation of name. The specific epithet is a patronym honouring Mr. Fermín Unzué, former manager of the El Soplao Cave, in recognition of his enthusiasm and interest in the study of El Soplao amber.

Material. CES-362, juvenile or adult female from El Soplao amber (Cantabria, Spain). The specimen has been preserved with high fidelity, although the thoracic region of the carapace has a posteromedial V-shaped depression that

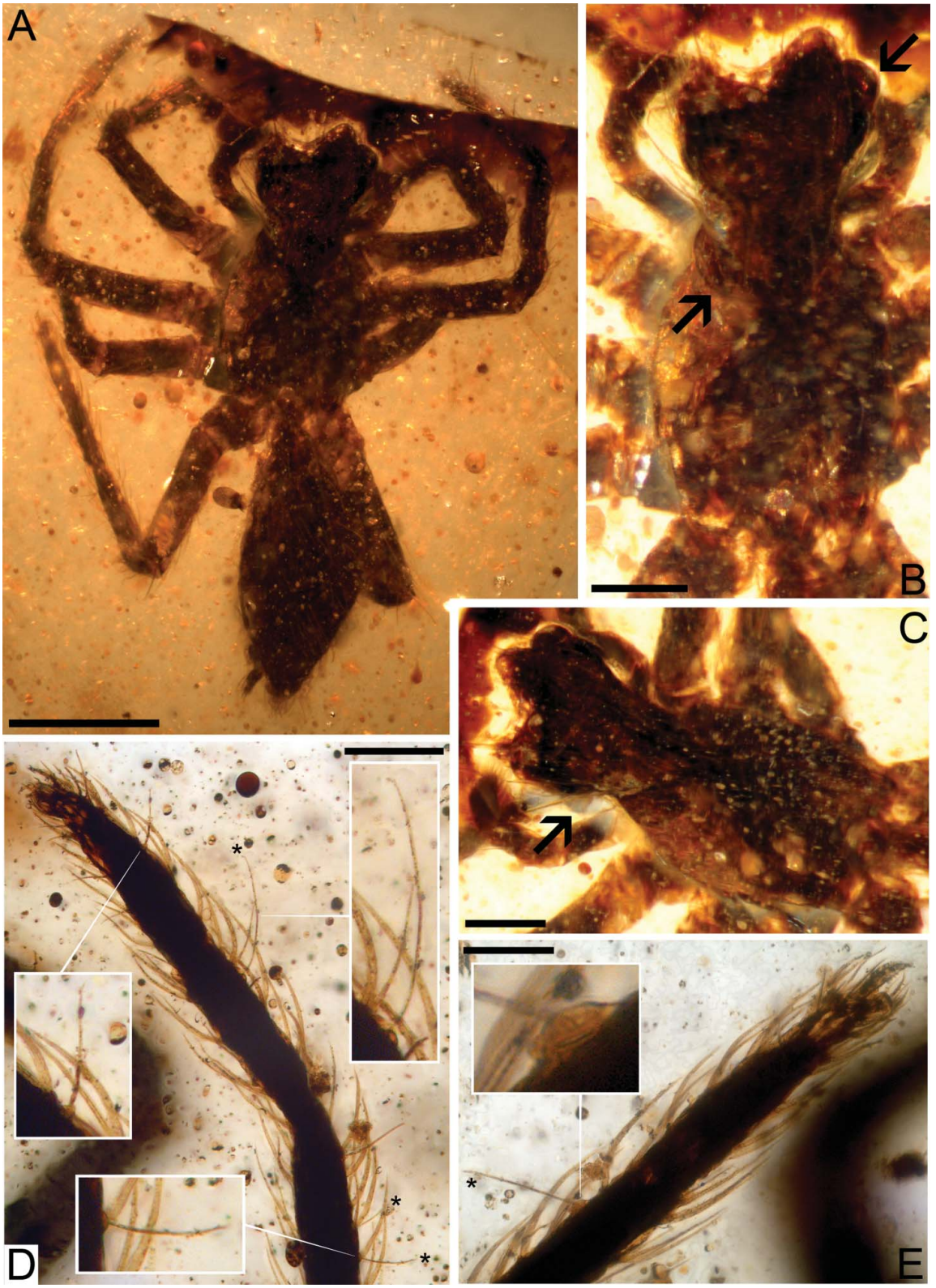

Figure 8. *Soplaogonomegops unzuei* gen. et sp. nov., CES-362; **A,** dorsal habitus; **B,** dorsal view of the carapace; note the PME (upper arrow) and the semicircular suture at the base of the neck (lower arrow); **C,** oblique view of the carapace; note the tip of the left chelicera (arrow); **D,** left ti, mt, and ts 2, showing trichobothria on ti (one is magnified at the bottom), a single trichobothrium on distal mt (magnified at the top right), and tactile setae (one magnified at the left); **E,** right mt and ts 2, showing tactile setae and a trichobothrium on distal mt with a very conspicuous bothrium (magnified in the detailed image). Scale bars: A = 0.5 mm; B, C = 0.2 mm; D, E = 0.1 mm.

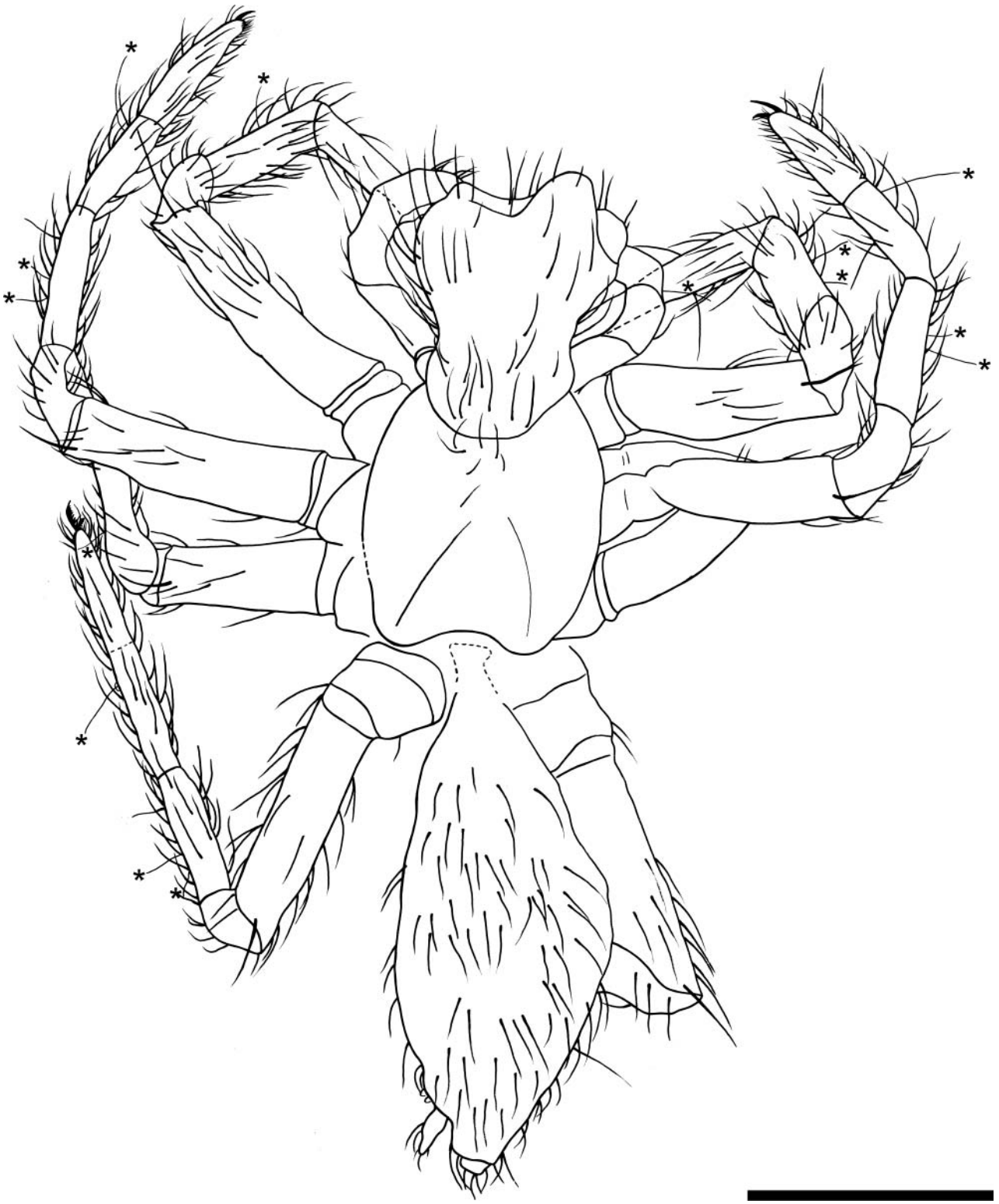

Figure 9. Camera lucida drawing of *Soplaogonomegops unzuei* gen. et sp. nov., CES-362. Scale bar = 0.5 mm.

creates two acute, symmetrical posterolateral lobes (interpreted as artefacts caused by taphonomic pressure rather than a true character), and the anteroventral part of the opisthosoma is depressed. The amber piece contains abundant minute bubbles.

Description. Body *c*. 2.10 mm long (Fig. 8A). Carapace very elongated (Fig. 8B, C); *c*. 1.00 mm long, 0.49 mm wide at widest point at proximal third, height not accurately measurable but >0.40 mm. Cephalic region of carapace distinct, projected forward *c*. 0.30 mm beyond the mouthparts and *c*. 0.18 mm beyond the chelicerae insertion (Fig. 8C). Cephalic region constricted in a neck, with narrowest point medially; *c*. 0.57 mm long, 0.25 mm wide at maximum width. Carapace slope decreasing at the base of the neck, where a semicircular suture delimits the cephalic and the thoracic regions of the carapace (Fig. 8B). Neck flaring out towards suture base. Anterolateral protrusions of the carapace relatively large, *c*. 0.25 mm in diameter; frontal depression created by the anterolateral protrusions moderately pronounced and rounded (not acute), 0.07 mm long, 0.28 mm wide. Thoracic region of the carapace gradually rising towards the cephalic region, *c*. 0.45 mm long. Fovea absent. Carapace clothed with anteriorly directed, plumose setae, up to 0.18 mm long. Chelicerae subconical, straight, barely posteriorly directed; 0.39 mm long, 0.22 mm broad at base; cheliceral insertion distinctly separated from the mouthparts in the vertical plane (chelicerae inserted at an elevated point of the carapace). Fang *c*. 0.22 mm long. Ental margin of cheliceral unguis with three/four visible peg teeth, 0.05−0.07 mm long. Single, erect, particularly elongated setae dorsoproximally on chelicerae, 0.15 mm long. Cheliceral stridulatory files not visible or absent. Chelicerae covered with plumose setae, 0.06 mm long. Only the PME visible (Fig. 8B), 0.12 mm in diameter; situated on the anterolateral protrusions of the carapace, slightly anteriorly directed; strongly sclerotized ring around PME not conspicuous. Labium subtriangular, wider than long, with all apices rounded; 0.10 mm long, 0.13 mm wide at base. Endites elongated, subtriangular, converging and almost meeting at the midline; 0.18 mm long, 0.05 mm wide at base; serrula well developed. Sternum shield-shaped, slightly longer than wide; 0.41 mm long, 0.31 mm wide at widest point at about two-thirds of its length; marginal projections not evident; distal end between cx 4 rounded; without tubercles; covered in abundant setae. Opisthosoma elongated and narrow, not sclerotized; *c*. 1.10 mm long, 0.42 mm wide as preserved, height not measurable; clothed in plumose setae, 0.09−0.13 mm long. Six spinnerets present in terminal position; ALS and PLS well developed, composed of two cylindrical segments, a larger proximal one, 0.10 mm long, 0.06 mm broad at tip, and a smaller distal one, 0.05 mm long, 0.03 mm wide; ALS close together; PLS separated by 0.14 mm; PMS small, 0.03 mm wide, length not measurable. Anal tubercle prominent, 0.04 mm long, 0.05 mm wide; covered in short, plumose setae, 0.05 mm long.

Legs relatively short, no legs enlarged. Ts shorter than mt. Legs 1, 2 and 4 subequal in length, so leg formula uncertain. Leg 3 the shortest. Leg 1 cx 0.07 mm, tr 0.13 mm, fe 0.42 mm, pt 0.15 mm, ti 0.24 mm, mt 0.32 mm, ts 0.30 mm, total 1.63 mm; leg 2 cx + tr 0.21 mm, fe 0.45 mm, pt 0.20 mm, ti 0.26 mm, mt 0.30 mm, ts 0.24 mm, total 1.66 mm; leg 3 cx 0.07 mm, tr 0.13 mm, fe 0.36 mm, pt 0.15 mm, ti 0.22 mm, mt 0.19 mm, ts 0.18 mm, total 1.30 mm; leg 4 cx + tr 0.18 mm, fe 0.49 mm, pt 0.16 mm, ti 0.27 mm, mt 0.27 mm, ts 0.26 mm, total 1.63 mm. Three tarsal claws; paired claws 0.05 mm long, with 12 visible teeth; median claw hook-like; onychium absent. Absence of setal scopulae or bristle-based non-scopular structures on mt and ts 1 + 2; a single ventral stiff bristle-like seta present on right mt 1 + 2. Two visible stiff bristle-like setae prolaterally on right ts 2, single bristle-like seta visible retrolaterally on right mt 1 + 2. Legs covered in plumose setae, up to 0.12 mm long. Dense, short, sinuous plumose/serrated setae below the claws on all legs; 0.03 mm long. Faint (almost hair-like in thickness), erect, curved, plumose, bristle present on all distal femora; 0.18 mm long. Tarsal trichobothria absent. Trichobothria conspicuously plumose, dorsally on all ti and mt as follows (Fig. 8D, E): (1) two on ti, 0.10 mm long: one at four- to five-tenths of its length and one at six-tenths of its length, more proximally placed on legs 3 + 4; and (2) one elongated at eight-tenths of mt, 0.13 mm long. Tactile setae dorsally and ventrally on all mt and ts as follows (Figs 8D−E): (1) one dorsally on distal ti, 0.06 mm long; (2) one dorsally on distal mt, 0.06 mm long; (3) one/two dorsally on distal ts, 0.06 mm long; (4) at least, one ventrally on distal mt, 0.05 mm long; and (5) up to three/four ventrally beyond three-fifths of ts, very short, 0.04 mm long.

Palpus slender; fe 0.19 mm long, pt + ti 0.18 mm long, ts 0.17 mm long; bristles absent; with a long trichobothrium at seven- to eight-tenths of ti, 0.10 mm long. Palpal claw absent. Plumose setae present, 0.08 mm long.

Remarks. The distinct carapace morphology of CES-362 warrants erection of a new genus based on two characters. First, the specimen is the only known lagonomegopid that possesses such a dramatic constriction of the cephalic region (i.e. neck). The cephalic region can be constricted in the genus *Burlagonomegops*, but without forming a distinctive neck (Penney 2005, 2006), while constriction into a neck is only found within Palpimanoidea in some archaeids (e.g. Forster & Platnick 1984; Wood 2008). Second, the semicircular suture delimiting the cephalic region from the thoracic region of the carapace in *Soplaogonomegops unzuei* gen. et sp. nov. has not been described from any other lagonomegopid. Within Palpimanoidea, this character is highly diagnostic of the fossil genus *Spatiator* Petrunkevitch, 1942 from Baltic amber

(Petrunkevitch 1942; Wunderlich 2004) but also present in some undescribed Baltic archaeids (pers. obs.). We note that the isolated bristles present on the mt and ts of legs 1 + 2 may be homologous with the numerous non-scopular bristles present in *Spinomegops*.

Discussion

Affinities of the family

Two characters, the presence of peg teeth and an elevated cheliceral gland mound, were used by Forster & Platnick (1984) as support for an expanded superfamily Palpimanoidea. This enlargement has been controversial, however, and some groups included by these authors have been removed based on subsequent molecular and morphological studies (e.g. Schütt 2000; Griswold *et al*. 2005; Rix *et al*. 2008; Rix & Harvey 2010). When Eskov & Wunderlich (1995) erected Lagonomegopidae, they placed the family in Palpimanoidea based on the combination of the following characters: (1) presence of peg teeth (Fig. 10A); (2) absence of (true) teeth on the cheliceral promargin; (3) nearly spineless legs; and (4) trichobothrial pattern (i.e. some trichobothria on the ti, even paired, a single one on the mt, and no tarsal trichobothria). The presence of peg teeth (character 1), although highly characteristic of Palpimanoidea (but absent in some groups such as Stenochilidae Thorell 1873), may be homoplastic and thus unreliable for systematic endeavours. For instance, peg teeth are present in some thomisids, periegopids and some mimetids (if the last are considered outside of palpimanoids) (Platnick 1976; Ono 1980; Forster & Platnick 1984; Platnick & Shadab 1993). True teeth (character 2) are lacking in many spider families (Jocqué & Dippenaar-Schoeman 2006). Characters 3 and 4 have been invalidated by subsequent lagonomegopid discoveries, as in the current paper. *Spinomegops* gen. nov. is characterized by the presence of numerous bristles on mt and ts 1 + 2, rendering character 3 variable. The trichobothrial pattern (character 4) can differ from that found within Palpimanoidea, i.e. a few on the ti and a single one (subdistal) on the mt (Forster & Platnick 1984). For example, the presence of tarsal trichobothria is currently one of the diagnostic characters for the genus *Burlagonomegops* (Penney 2005, 2006). The holotype and paratype of *B. eskovi* have ts with one long median and one short distal trichobothrium (Penney 2005), whereas *B. alavensis* possesses two to four trichobothria along all ts and more than a single (up to three) trichobothria on most mt (Penney 2006, fig. 2B). Although tarsal trichobothria are considered diagnostic, Wunderlich (2008) described several Burmese specimens attributed to *B.* ?*eskovi* that appear to lack this character. He also noted that the presence of tarsal trichobothria and more than a single trichobothrium on the mt would be exclusive within Palpimanoidea (cf. Forster & Platnick 1984). As such, Wunderlich (2008) regarded these trichobothria as non-trichobothrial hairs. Examination of the *B. alavensis* holotype (Fig. 10B, C) confirms the presence of numerous thin, very elongated, flexible, hair-like structures emerging perpendicular to the dorsal surface of the mt and ts of different legs. Since the shape of these structures mirrors the numerous trichobothrial hairs emerging from the ti (Fig. 10B), which are typical in lagonomegopids and the whole of Palpimanoidea (Forster & Platnick 1984), and fulfil the criteria detailed in the Trichobothria determination section, their status as trichobothria should be considered valid.

The above-mentioned four characters used by Eskov & Wunderlich (1995) for placing lagonomegopids within Palpimanoidea seem weak, and we refrain from identifying closest relative(s) for the group. Nevertheless, the diversity detailed herein revealed a variety of characters also found in palpimanoids, i.e. those characters concerning morphology of the carapace, eye arrangement, and presence of cuticular specializations on mt and ts 1 + 2, which are discussed below.

Carapace morphology. Two basic carapace morphologies can be distinguished within Palpimanoidea regarding point of cheliceral insertion: (1) true raising of the cephalic region, with chelicerae inserted at an elevated point on the carapace, resulting in clear vertical separation from the mouthparts (endites and labium) (see Forster & Platnick 1984); and (2) chelicerae not placed at an elevated point on the carapace, but rather close to the mouthparts vertically, at approximately the level of the sternum (pers. obs.). The former condition occurs in the palpimanoid families Archaeidae Koch & Berendt, 1854 and Mecysmaucheniidae Simon, 1895, whereas the latter occurs in the palpimanoid families Huttoniidae Simon, 1893, Palpimanidae Thorell, 1870, and Stenochilidae. The carapace shape is variable within Lagonomegopidae and both types of carapace morphologies co-exist. The first type, in which the chelicerae are inserted at an elevated point of the carapace, is present in the two species of *Burlagonomegops*, *Lagonomegops*? *cor* sp. nov., *Spinomegops arcanus* sp. nov., *Soplaogonomegops unzuei* gen. et sp. nov., and perhaps *Zarqagonomegops wunderlichi*, whereas the second type is present in *Grandoculus chemahawinensis* and *Lagonomegops sukatchevae* (see Eskov & Wunderlich 1995, figs 3, 4). We are unable to ascertain this character in *Lagonomegops americanus*.

Another prosomal trait present in lagonomegopids and also palpimanoids is the constriction of the cephalic region (neck) in *Soplaogonomegops unzuei* gen. et sp. nov. found in archaeids (Forster & Platnick 1984; Wood 2008). Additionally, as mentioned, some Baltic archaeids have a semicircular suture delimiting the cephalic and thoracic regions of the carapace (pers. obs.), as occurs in *S. unzuei*. This character is also present in species of the palpimanoid genus *Spatiator*, currently classified as a family exclusively known from

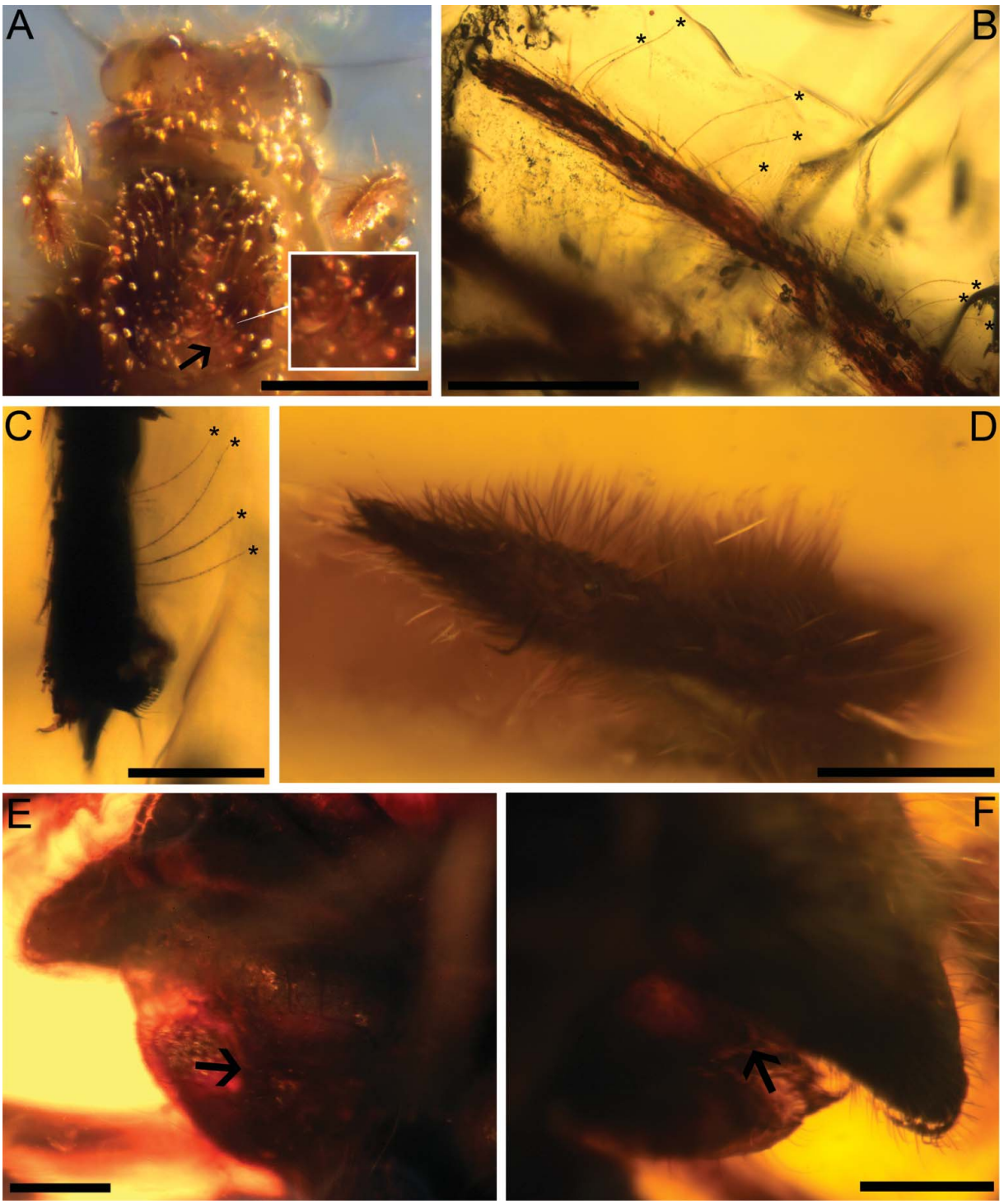

Figure 10. A–C, *Burlagonomegops alavensis* Penney, 2006, MCNA-8635, holotype from Álava amber, Peñacerrada II outcrop (Álava, Spain); **A,** frontoventral view of the cephalic region of the carapace; note the pair of large PME and the four visible peg teeth on the cheliceral unguis (arrow), magnified in the detailed image; **B,** left ti (distal part), mt, and ts 3 and their visible trichobothria; **C,** distal part of left leg 4; note the presence of, at least, three tarsal trichobothria. **D–F,** *Grandoculus chemahawinensis* Penney, 2004, MCZ-A-5000, holotype from Cedar Lake amber (Manitoba, Canada); **D,** prolateral scopulae of setae visible on left mt (right) and ts (left); note how the tips of the metatarsal scopular setae appear to be distinctly curved; **E,** ventral view of the anterior part of the prosoma, showing chelicerae (top left) and mouthparts (bottom right); the arrow marks the tip of the labium, where the endites meet at the midline; **F,** dorsal view of the anterior part of the prosoma, showing chelicerae (top right) and mouthparts (bottom left); the arrow marks the tip of the labium, where the endites meet at the midline. Scale bars: A, B = 0.5 mm; C, D, E, F = 0.2 mm.

Baltic amber (e.g. Wunderlich 2006). Recent archaeids and some fossils may also possess a distinct cheliceral bristle on the proximal part of the chelicerae (Forster & Platnick 1984; Penney 2003), which is similar to the elongated, erect setae identified in *Spinomegops arcanus* sp. nov., *S. aragonensis* sp. nov. (Fig. 6B) and *S. unzuei*.

Eye arrangement. Eye homology is uncertain in lagonomegopids, and we tentatively employ the suggested nomenclature of Eskov & Wunderlich (1995). These authors assumed two recurved and very wide eye rows, with small and contiguous AME and ALE in the anterior row and a posterior row with large PME and small PLE well separated from the PME. Within Lagonomegopidae, eyes other than the large anterior eyes have been difficult to discern due to small size and variable position, often concealed by the anterolateral protrusions of the carapace. In the most recent diagnosis for the family (Wunderlich 2008), the presence of eight eyes was omitted, since six eyes were indicated for the genera *Lagonomegops* and *Zarqagonomegops*, and four eyes were noted for the remaining genera (*Burlagonomegops* and *Grandoculus*). Though eight eyes were described from *Lagonomegops sukatchevae*, the small eye below the PME (either the AME or the ALE) was considered dubious (Eskov & Wunderlich 1995). These authors noted that the lagonomegopid eye pattern seemed unique within Araneae. However, the eye conformation of *Spinomegops aragonensis* sp. nov. (Figs 6C–D, 7) (matching that of *Lagonomegops sukatchevae* if this specimen possessed eight eyes) resembles that found in Archaeidae (see Forster & Platnick 1984; Wood 2008), where the eyes are placed in two wide, laterally disposed eye rows, with a pair of anterior eyes the largest (although not as dramatically enlarged as in lagonomegopids) and two smaller, contiguous eyes placed below. The only significant difference between archaeid and lagonomegopid eye arrangement is that lagonomegopids have a posteriormost small eye (interpreted as the PLE) far beyond the other eyes, perhaps even in a separate, third row, whereas in archaeids the potentially homologous eye (considered the PME) is much closer. Roughly the same archaeid eye pattern occurs in *Lacunauchenius speciosus* Wunderlich, 2008 from late Albian amber from Myanmar, placed within the subfamily Lacunaucheniinae Wunderlich, 2008 and closely related to modern archaeids and mecysmaucheniids (Wunderlich 2008).

Mouthparts. Although the lagonomegopid eye pattern is potentially congruent with archaeids, their mouthpart morphology resembles that found in Mecysmaucheniidae. In both groups, the labium is wider than long, triangular, with the endites directed across the labium and almost meeting at the midline. Lagonomegopids, however, lack chelicerae originating from a foramen in the carapace, an important diagnostic character potentially uniting Archaeidae and Mecysmaucheniidae (Forster & Platnick 1984).

Cuticular specializations on legs 1 + 2. Members of the genera *Grandoculus* and *Spinomegops* gen. nov. have cuticular specializations on the distal podomeres of legs 1 + 2, scopular in the former (composed of dense setae) and non-scopular in the latter (composed of sparse bristles). Within Palpimanoidea, the families Huttoniidae, Palpimanidae and Stenochilidae possess spatulate setae (specialized setae with an expanded distal plate) on distal podomeres of legs 1 + 2. These specialized setae form dense scopulae in Palpimanidae and Stenochilidae, whereas only a few rows are present in the Huttoniidae (Forster & Platnick 1984). Cuticular specializations on legs have been described from some modern archaeids, but representing just one or two rows of setae with slight lateral expansions (Forster & Platnick 1984). The scopulae of spatulate setae have been shown to improve the raptorial ability of spiders belonging to the genus *Palpimanus* (Palpimanidae) when hunting (Pekár *et al*. 2011), and prolateral spines with a raptorial function also exist in the Mimetidae (Platnick & Shadab 1993). Hence, perhaps the structures found in *Grandoculus* and *Spinomegops* were used for a similar function.

The family Grandoculidae

Penney (2011) erected the family Grandoculidae to accommodate *Grandoculus chemahawinensis*, previously considered a lagonomegopid by Penney (2004) (see also Penney & Selden 2011), using the following diagnosis: "[1] Raised cephalic region with a bulge on each side antero-laterally bearing a large eye [2] with a much smaller eye located below it; [3] chelicerae elongate and procurved. [4] Leg I distinctly longer and more robust than the others, with very closely packed, long, hook-tipped scopular hairs on the prolateral surface of the metatarsus, and long, straight, pointed scopular hairs on the prolateral surface of the tarsus (both these scopulae forming dense brushes); tibia of leg II with short scopulae along most of its length; [5] legs without spines and [6] palpal tarsus lacking a claw."

Features 1 and 6 are diagnostic of Lagonomegopidae. Penney (2011) indicated that character 2 distinguishes *G. chemahawinensis* from other lagonomegopids, including *Lagonomegops sukatchevae*. Four eyes, however, are present (or, at least, visible) in *Burlagonomegops eskovi* and *Lagonomegops*? *cor* sp. nov., both of which lack scopulae. Regarding feature 3, *Lagonomegops*? *cor* and *Spinomegops aragonensis* sp. nov. have very similar prosoma/chelicerae length ratios, around 2–2.5, and similarly procurved chelicerae, especially the latter species (Figs 2C, 6B). Character 5 is also invalidated after re-observation of the holotype, since an erect, curved spine is visible on left fe 1 (the specimen only has left legs 1–3 preserved beyond the femora). Furthermore, although not included in the diagnosis, the mouthparts of *G. chemahawinensis* were also employed as evidence for erecting the new family.

Table 1. Character distribution among current lagonomegopid genera.

	Lagonomegops Eskov & Wunderlich, 1995	*Grandoculus* Penney, 2004	*Burlagonomegops* Penney, 2005	*Zarqagonomegops* Kaddumi, 2007	*Spinomegops* gen. nov.	*Soplaogonomegops* gen. nov.
Number of visible eyes	Up to 6 (8?)	4	4	6	Up to 8	2
Cephalic region projected forwards	Absent	Absent	Present	Absent	Present/absent*	Present
Cephalic region constricted	Absent	Absent	Present	Absent	Absent	Present (forming a neck)
Cephalic region semicircular suture	Absent	Absent	Absent	Absent	Absent	Present
Enlarged leg 1	Absent	Present	Absent	Absent	Absent	Absent
Cuticular specializations on legs 1 + 2	Absent	Present (scopular)	Absent	Absent	Present (non scopular)	Absent
Tarsal trichobothria	Absent	Absent	Present	Absent	Present/absent*	Absent

*Present in *S. aragonensis*. See genus Remarks herein.

Penney (2011) noted that the endites of *G. chemahawinensis* were not directed across the labium, and the latter was not triangular as in other lagonomegopids. Re-analysis of the holotype, however, revealed that the labium is, indeed, triangular, with two converging endites (Fig. 10E). This occurs in *Lagonomegops sukatchevae*, type genus and species of the family Lagonomegopidae (Eskov & Wunderlich 1995, fig. 7). The right endite was likely misinterpreted as the labium by Penney (2004, 2011). Although barely visible in ventral view, the mouthparts of G. *chemahawinensis* can be seen in dorsolateral view (Fig. 10F). Additionally, although a single metatarsal trichobothria was described from *G. chemahawinensis*, some trichobothria, most likely arranged in two pairs, can be seen proximally on left leg 2. Consequently, the aforementioned features (1–3, 5–6) do not support granting *G. chemahawinensis* familial rank. Only feature 4 distinguishes *G. chemahawinensis* from other described lagonomegopids (Table 1), i.e. an enlarged first pair of legs and distinct cuticular specializations on legs 1 + 2, which correspond to hairs forming scopulae (= brushes) on the prolateral surface of mt and ts 1 (hairs hooked-tipped on the mt 1; Fig. 10D) and ti 2.

The two new species classified within *Spinomegops* gen. nov. are potentially related to *G. chemahawinensis* because they also have cuticular specializations on legs 1 + 2, i.e. numerous, elongated bristles (spine-like to almost hair-like in thickness) not forming scopulae (loosely arranged) on the pro- and retrolateral surface of the mt and ts 1 + 2. Nevertheless, we avoid classifying them within Penney's Grandoculidae or creating a new family because these taxa possess additional characters differentiating them from *G. chemahawinensis* and uniting them with lagonomegopids. Indeed, *S. aragonensis* clearly possesses eight eyes (Fig. 6C, D), the number reported as possibly present in *Lagonomegops sukatchevae* (Eskov & Wunderlich 1995, figs 3, 4). Moreover, *S. aragonensis* has tarsal trichobothria and a raised cephalic region with chelicerae inserted at an elevated point in the carapace. Both of these characters are present in the genus *Burlagonomegops* which, in turn, lacks cuticular specializations on legs 1 + 2 (Table 1). Therefore, the presence of distinctive cuticular specializations on legs 1 + 2 may not warrant familial status, and we hypothesize these structures are homologous in the genera *Grandoculus* and *Spinomegops*.

Penney may be correct in separating *G. chemahawinensis* from other lagonomegopids based on this character; however, elevating taxa to higher ranks seems prudent only when done in a phylogenetic framework (Penney & Selden 2011; Wiley & Lieberman 2011). Since the relationships within Lagonomegopidae and among potentially related taxa are not understood, we refrain from further splitting until more diversity is uncovered and/or quantitative analyses performed. We here consider Grandoculidae Penney, 2011 a junior synonym of Lagonomegopidae Eskov & Wunderlich, 1995.

Conclusions

With the taxa described herein, Spanish amber currently holds the greatest diversity of Lagonomegopidae. Our study supports the notion that lagonomegopid diversity was high during the Cretaceous, corresponding with a widespread distribution, at least in the Northern Hemisphere. Despite high diversity and a large geographical range, the group appears to have gone extinct by the end of the Cretaceous.

The placement of the family Lagonomegopidae within the superfamily Palpimanoidea remains controversial. The primary evidence supporting this affiliation is the diverse combination of important, possibly diagnostic, characters shared by lagonomegopids and different groups of palpimanoids. Our knowledge of these characters has been substantially improved with the taxa described herein. If lagonomegopids are considered palpimanoids, the lineage is most likely basal or sister to other palpimanoid lineages.

The family Grandoculidae is synonymized with Lagonomegopidae. The presence of cuticular structures on the legs does not warrant familial rank for *Grandoculus chemahawinensis*, as new taxa described herein possess this character and also present other characters diagnostic of lagonomegopids.

Although the discovery of these fossils has increased our knowledge of Lagonomegopidae, it remains insufficient for a phylogenetic analysis of the family. A future assessment using taxa yet to be discovered will be essential for providing validity to existing genera and for testing the palpimanoidean nature of this group.

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