



A PRESUMED SPELAEGRIPHACEAN CRUSTACEAN FROM AN UPPER BARREMIAN WETLAND (LAS HOYAS; LOWER CRETACEOUS; CENTRAL SPAIN)

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Typescript received 20 May 2011; accepted in revised form 25 August 2011

Abstract: A third fossil attributable to the crustacean peracarid order Spelaeogriphacea is described from an Upper Barremian (125 Ma) lacustrine environment in Central Spain. Neither the new taxon, *Spinogriphus ibericus* gen. et sp. nov., nor the two already described fossil forms can be identified with certainty as crown-group spelaeogriphaceans. We consider that Schram's 1974 family Acadiocarididae represents stem-lineage spelaeogriphaceans and should accommodate these fossil taxa that display very generalised peracaridan features and lack any conspicuous autapomor-

phies, except for a short carapace, undifferentiated pereopods, foliaceous pleopods and a tail fan-like (uropods + telson) caudal structure where the unsegmented uropodal endopod lacks annulation. The zoogeography of the Acadiocarididae is Laurasian in contrast to the modern, crown-group spelaeogriphaceans (Spelaeogriphidae), which are limited to Gondwanan territories.

Key words: Crustacea, Peracarida, Spelaeogriphacea, Acadiocarididae, Biogeography, Las Hoyas, Iberia.

THE crustacean order Spelaeogriphacea Gordon, 1957 (Malacostraca: Peracarida) comprises four Recent eyeless species, all of them unpigmented and living exclusively in subterranean waters. They appear associated with freshwater in southern continents, in ancient cratons not affected by marine transgressions at least since the Early Cretaceous, when Gondwana started to break-up. *Spelaeogriphus lepidops* Gordon, 1957 inhabits two caves opening in Ordovician quartzites in South Africa (Gordon 1957, 1960), and *Potiicoara brasiliensis* Pires, 1987 dwells in caves in Upper Proterozoic limestone at Mato Grosso do Sul in Brazil (Pires 1987). The group is known also from Australia, where *Mangkurtu mityula* Poore and Humphreys, 1998 and *M. kutjarra* Poore and Humphreys, 2003 are recorded from borehole wells drilled in middle to late Tertiary calcretes in north-western Australia; however, these deposits overlie and are in direct contact with Lower Cretaceous alluvial conglomerates (Poore and Humphreys 1998, 2003). All these terrains were once part of Gondwana, and we infer that the penetration of spelaeogriphaceans into continental waters took place prior to the fragmentation of this supercontinent (starting c. 140 Ma), and that their current distribution pattern reflects plate tectonic history (Pires 1987).

The spelaeogriphacean body plan is rather featureless at first glance, and this makes the identification of fossils problematic, especially if limbs are not well preserved. Most spelaeogriphacean features correspond to what could be called a generalised malacostracan peracarid (Calman 1909) with a roughly cylindrical body, the cephalothorax incorporating the first thoracomere only (which carries a maxilliped provided with an epipodite), and lacking functional eyes (displaying eyestalks devoid of corneas). The antennule consists of a three-segmented peduncle plus two distal multi-articulate flagella, whereas the antenna is biramous and has a short scale-like exopod.

The pereion comprises seven free pereionites, each provided with a pair of biramous pereopods with stenopodial endopods; these pereopods are all similar, with the first pair hardly differentiated from the rest. The pleon consists of six free pleonites, each with a pair of well-developed foliaceous biramous pleopods. The last pair of limbs (uropods) combines with the free, articulated telson to form a fan-like tail structure. The uropodal exopod is two-segmented, whereas the endopod, contrary to the condition displayed in other peracarid orders such as mictaceans, bochusaceans or tanaidaceans, is unsegmented

and devoid of external annulation. As typical for peracarids, brooding female spelaeogriphaceans have a ventral marsupium formed by oöstegites (= foliaceous medial processes of the pereopodal coxae – see Boxshall and Jaume 2009).

The most remarkable autapomorphy of the Spelaeogriphacea is said to be the transformation of the exopods of the posterior pairs of pereopods into nonsetose, respiratory paddles (Grindley and Hessler 1971; Richter and Scholtz 2001). However, members of another peracarid group, the order Amphipoda, retain the so-called ‘coxal gill’ on pereopod 7 and also share this feature because this presumed gill is implanted on the basis and not on the coxa as in the true coxal gills of amphipod pereopods and consequently should be considered an exopod (Steele and Steele 1991). In addition, it is worth mentioning here that anaspidid syncarids carry a reduced respiratory exopodite as well as the two ordinary epipodites on the sixth pereopod (Smith 1909).

Another presumed characteristic of the group, the short, posteriorly directed carapace formed as an extension of the rear margin of the dorsal cephalothoracic shield and concealing part of the first pereonite appears to be identically developed in several thermosbaenacean taxa.

FOSSIL RECORD

The Spelaeogriphacea has a limited fossil record. Two fossil forms, from the Carboniferous of Canada and the Upper Jurassic of China, are treated as spelaeogriphaceans by some authors (Schram 1974; Shen *et al.* 1998, 1999), but none of these fossils preserves diagnostic features that allow us to classify them as anything other than generalised peracaridans. Brooks (1962) considered one of them, *Acadiocaris novascotica* (Copeland, 1957), as one of the two members of a new fossil order, the Anthracocaridacea, which he tentatively assigned to the Peracarida. Schram (1974) implicitly noted the heterogeneity of the Anthracocaridacea and the family Anthracocarididae when he recognised affinities between its type genus *Anthracocaris* Calman, 1932, and fossil tanaids such as *Cryptocaris sensu* Schram, 1974, and established a separate family, the Acadiocarididae within the Spelaeogriphacea, to accommodate *Acadiocaris*. The diagnosis of the Acadiocarididae was: no optic notch on carapace; thoracopodal endopods well developed; natatory pleopods on the first five pleomeres. Schram (1974) noted that no exopods were preserved on the thoracopods, and no scaphocerite (= exopodal scale) was detected on the antenna of any specimens. Schram (1974) regarded this fossil as representing a more primitive condition, in the lack of optic notches and the presence of a well-devel-

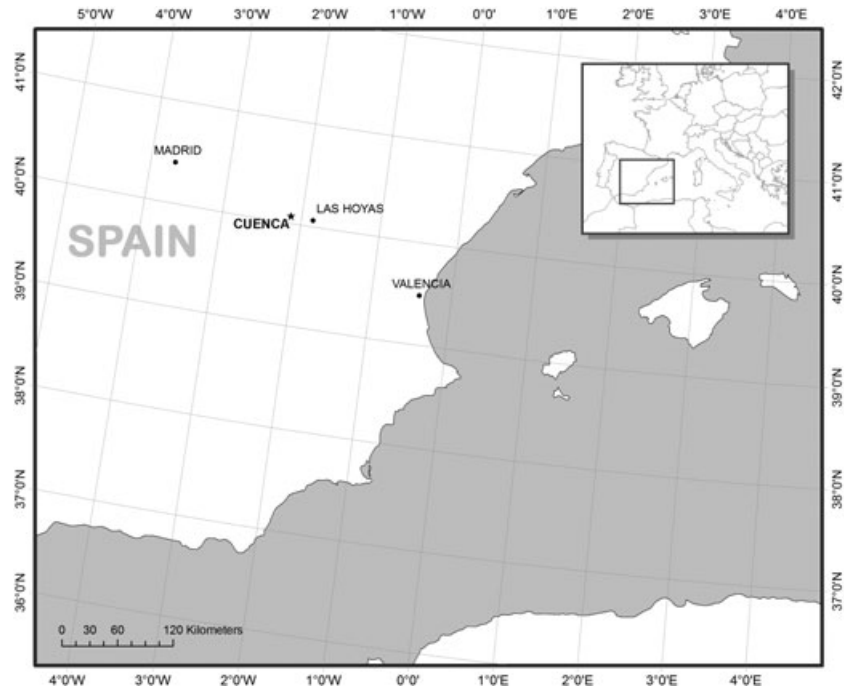
oped fifth pleopod, than exhibited in the modern family Spelaeogriphidae.

The Chinese *Liaoningogriphus quadripartitus* Shen, Taylor and Schram, 1998 was undeniably a freshwater form, as are all modern spelaeogriphaceans, but confusion remains on the habitat of the Canadian *Acadiocaris novascotica*. Copeland (1957, p. 595) explicitly stated in the original description of *Acadiocaris* that it was collected from strata of nonmarine origin. Notwithstanding that, Schram (1974) regarded this taxon as a near-shore marine form and, partially based on this statement, hypothesised that the current Gondwanan distribution of the order is an artefact produced by the extinction of those taxa formerly living in northern landmasses and in the sea, rather than the southern landmasses being the centre of origin of the group. Subsequently, Shen *et al.* (1998, p. 34) insisted on the marine condition of *Acadiocaris* – again without providing any supporting palaeoenvironmental data –, and even suggested that the sediments yielding it could have corresponded to a deep-water rather than a near-shore habitat.

Because the presence of crown-group Spelaeogriphacea in Laurasian territories would challenge the Gondwanan origin attributed to the group, any fossil discovery of presumed spelaeogriphaceans in Laurasia – or anywhere in marine sediments – would provide highly relevant evidence for solving this biogeographic dilemma.

We describe a third fossil form that could be attributed to the Spelaeogriphacea, again from a northern landmass: an Upper Barremian (125 Ma) lacustrine environment in Central Spain (Serranía de Cuenca, La Huérguina Formation). Originally recognised as a spelaeogriphacean by Eva Pinardo-Moya (1997, pers. comm.; cited in Poore and Humphreys 1998), this taxon has been mentioned in several papers dealing with both fossil and extant spelaeogriphaceans (Poore and Humphreys 1998, Shen *et al.* 1998), but had never been formally studied (Sanz *et al.* 2001). Unfortunately, neither the new taxon nor the two above-mentioned fossil forms can be identified with certainty as crown-group spelaeogriphaceans. We consider that Schram’s 1974 family Acadiocarididae represents stem-lineage spelaeogriphaceans and accommodates these fossil taxa that display very generalised peracaridan features but lack any conspicuous autapomorphies except for: a short carapace, undifferentiated pereopods, foliaceous pleopods and a tail fan-like (uropods + telson) caudal structure where the unsegmented uropodal endopod is devoid of annulation. The zoogeography of the Acadiocarididae is thus Laurasian and contrasts with that of modern, crown-group spelaeogriphaceans (Spelaeogriphidae), which are limited to Gondwanan territories. As discussed below, *Spinogriphus ibericus* gen. et sp. nov. is probably the oldest stygobiont crustacean recorded to date.

FIG. 1. Map showing location of Las Hoyas in central Spain.



GEOLOGICAL SETTING

Las Hoyas, located 30 km to the East of the city of Cuenca in Central Spain (Fig. 1), is a richly fossiliferous Upper Barremian palaeo-wetland associated with a subsiding basin away from any direct marine influence (Fregenal-Martínez 1998; Poyato-Ariza *et al.* 1998; Fregenal-Martínez and Melendez 2000; Fregenal-Martínez and Buscalioni 2009). The site is a konservat-Lagerstätte renowned for having delivered up some landmark fossils that were pivotal in our developing understanding of the early radiation of birds and the origin of their flight abilities (Sanz *et al.* 2002). In total, about 30 000 fossils representing a spectacular array of taxonomic groups, from prokaryotes to dinosaurs, many of them in an extraordinary state of preservation, have been unearthed from the site thus far (Fregenal-Martínez and Buscalioni 2009; Sanz *et al.* 2001). The palaeo-environment at Las Hoyas may have resembled the modern Florida Everglades, that is a mosaic of alluvial plains, marshy and swampy palustrine plains, channels, sloughs, ponds and shallow permanent lakes under a subtropical climate (Fregenal-Martínez and Buscalioni 2009). The fossil-bearing layers appear in a section of the deposit comprising laminated limestone composed almost entirely of calcium carbonate and presumably formed in a shallow, hardwater lake or pond subjected to strong, cyclical oscillations in water level (reduced to a few cm during periods of drought) and with the bottom covered with thick microbial mats. Geochemical data (Poyato-Ariza *et al.* 1998) suggest that the setting might be similar to that of a karstic lake

(i.e. subjected to groundwater influence), but conflict with sedimentological and palaeo-ichnological evidence that suggests that the lake sediments were anoxic or dysaerobic (Buatois *et al.* 2000). The entire deposit overlies Bathonian (Middle Jurassic) marine limestone that underwent strong karstification earlier and again during the continental Early Cretaceous sedimentation (Fregenal-Martínez and Melendez 2000).

MATERIAL AND METHODS

Specimens appear isolated or in pairs, as variably stretched films or inclusions preserving some relief, always entire and with fully articulated body somites and limbs; some expose traces of their internal anatomy (gut tract). Their bodies appear fragile, and none shows traces of having been transported over long distances, from which we infer that all lived close to their burial place. Specimens were photographed in the laboratory at high resolution enabling subsequent zooming on relevant structures: high-angle illumination and a macro-lens were used. To increase contrast, the colour of the images was artificially changed using Adobe Photoshop® and then converted to grayscale. Natural colour images are available from the authors. Details revealed by photographs were also studied directly on the specimens using a Leica MZ16 stereomicroscope. All specimens are deposited in the Las Hoyas collection at the Museo de las Ciencias de Castilla-La Mancha (MCCM-LH; Cuenca; Spain). The higher (supra-family) level classification follows Martin and Davis (2001).

SYSTEMATIC PALAEOLOGY

Superclass CRUSTACEA Brünnich, 1772
 Class MALACOSTRACA Latreille, 1802
 Subclass EUMALACOSTRACA Grobben, 1892
 Superorder PERACARIDA Calman, 1904
 Order SPELAEOGRIPHACEA Gordon, 1957
 Family ACADIOCARIDIDAE Schram, 1974

Genus SPINOGRIPHUS gen. nov.

Diagnosis. Anterolateral margin of cephalothoracic shield without notch separating lateral from dorsal parts. Eye-stalks lacking. Endopodal segments of antenna equal in length; scale-like antennal exopod well developed, as long as proximal endopodal segment; antennal flagellum geniculate (=reflexed) at base. Pleopod 5 not reduced. Distal margin of proximal exopodal segment of uropod lined with row of stout spines; uropodal endopod short (much shorter than corresponding exopod). Telson short (reaching only as far as distal margin of uropodal protopod), provided with long (about half as long as telson) spines.

Derivation of name. The new genus name refers to the telson of the new taxon, which is provided with long, stout spines. The termination *-griphus* appears in the genus name of the first described spelaeogriphacean, *Spelaeogriphus lepidops*.

Type species. *Spinogriphus ibericus* sp. nov. by original designation.

Distribution. As for the only species known thus far, described below.

Spinogriphus ibericus sp. nov.

Figures 2–6

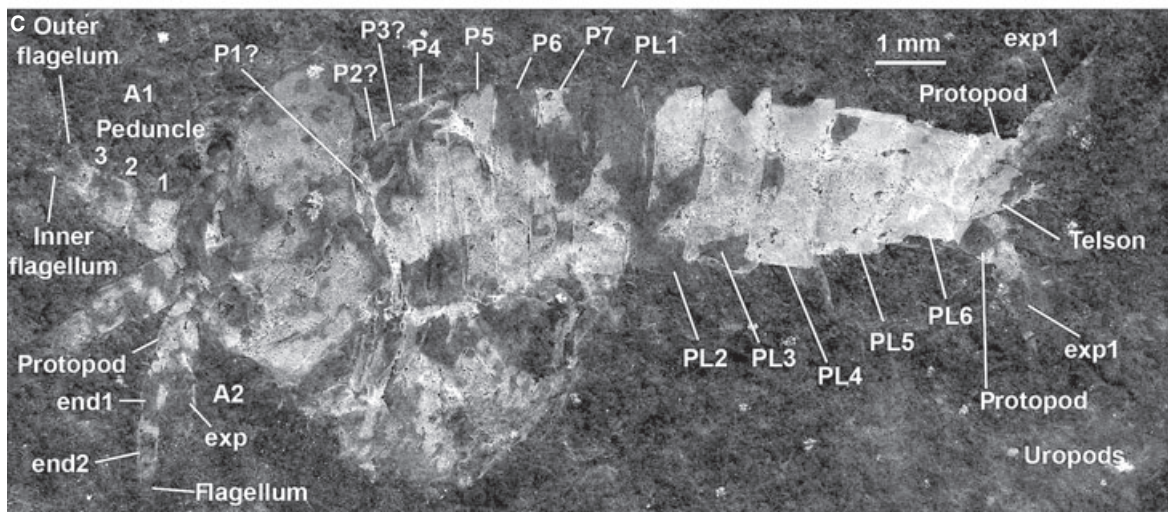
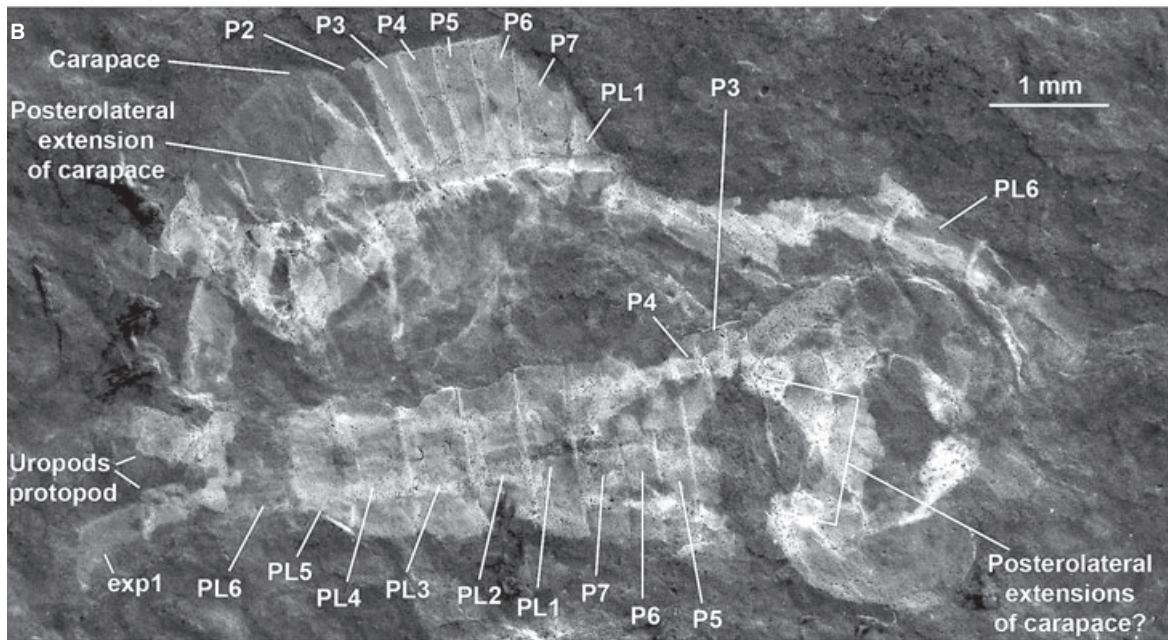
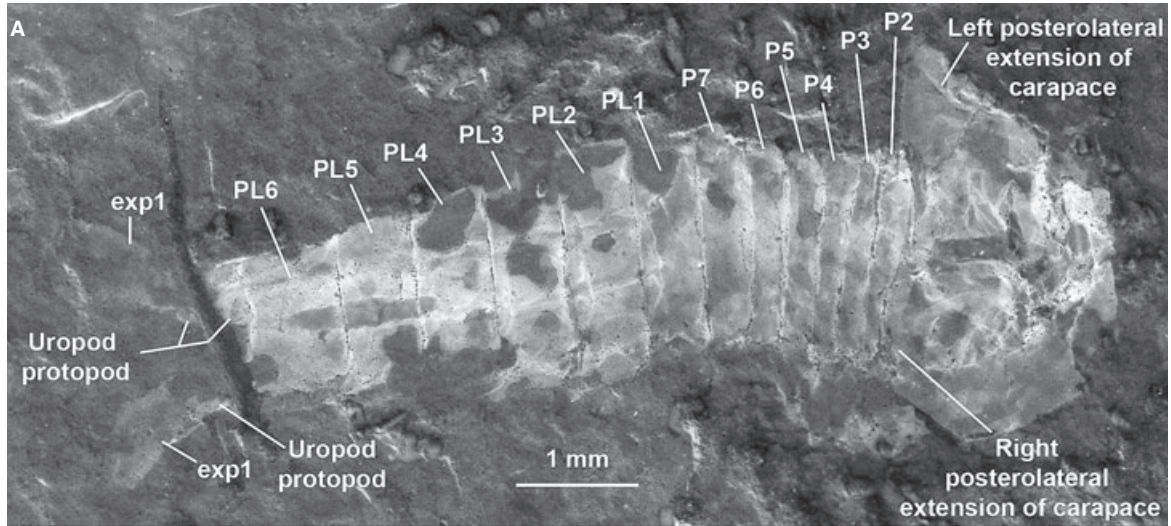
Holotype. MCCM-LH 16042a (Fig. 3B); specimen in lateral aspect showing body tagmosis with first pereionite exposed beside stretched carapace, traces of presumed pereipodal exopods, relative proportions of pleopodal protopod and exopod, and presumed spine at distolateral angle of protopod of pleopod.

Paratypes. MCCM-LH 1784b (Fig. 5D): Specimen apparently in ventral aspect showing antennules, antennae with antennal scales, protopods of uropods and vestige of telson. MCCM-LH

1979 (Fig. 4D): Specimen in dorsal aspect showing carapace and antennae with exopodal scale and geniculate flagellum. MCCM-LH 2194b (Fig. 2B): Two specimens, one in dorsal aspect, other in lateral, showing body tagmosis, posterolateral extensions of carapace and proximal part of uropods. MCCM-LH 2195b (Fig. 2A): specimen in dorsal aspect showing body tagmosis, posterolateral extensions of carapace and proximal part of uropods. MCCM-LH 7302a (Fig. 4C): Specimen apparently in ventral aspect showing antennules and antennae with antennal exopod attached. MCCM-LH 8144a (Fig. 2C): Specimen in dorso-lateral aspect showing segmentation of antennular and antennal peduncles, presumed two flagella on antennule, extent of pereipods, trace of a pleopod, uropods retaining protopod and with proximal exopodal segment displaying some marginal spines, and telson with distal spines. MCCM-LH 13221a: Specimen in dorsal aspect showing gut contents. MCCM-LH 13531 (Fig. 4A): Specimen in dorsal aspect showing bi-flagellate antennule, geniculate flagellum of antenna, pereipods, foliaceous pleopods and shape of uropod. MCCM-LH 13536: Specimen in lateral aspect with traces of foliaceous pleopods. MCCM-LH 15083a (Fig. 3A): Specimen in lateral aspect showing epimeral plates and retaining pleopods and traces of pereipods. MCCM-LH 15298 (Fig. 4B, E): Specimen in dorsal aspect showing body tagmosis with exposed pereionite 1, traces of gut tract, and uropods with strongly spinose medial and distal margins of proximal segment of exopod. MCCM-LH 16042a (Fig. 3B): Specimen in lateral aspect showing body tagmosis with exposed pereionite 1, traces of pereipodal exopods and foliaceous pleopods. MCCM-LH 16042b (Fig. 3C): Specimen in lateral aspect showing carapace, foliaceous pleopods and two-segmented exopod of uropods. MCCM-LH 17054 (Fig. 5C): Specimen in lateral aspect showing expanded protopod of pleopods and presumed spines of telson. MCCM-LH 17349a (Fig. 5A): Specimen in dorsal aspect exposing pereipods on both sides. MCCM-LH 21253a (Fig. 5F): Specimen in dorsal aspect showing segmentation of antennular peduncle, antennal peduncle with attached exopod, and segmentation of uropods. MCCM-LH 26953a (Fig. 4F): Specimen in dorsal aspect showing spinose margin of telson. MCCM-LH 26953b (Fig. 5E): Stretched specimen showing posterior pleopods, stout spines on inner margin of proximal exopodal segment of uropod, and traces of long marginal spines on telson. A total of 17 specimens.

Additional material examined. MCCM-LH 7011b: Specimen in dorsal aspect. MCCM-LH 7207b: Specimen in lateral aspect with pereipods exposed. MCCM-LH 7209a: Specimen in lateral aspect showing two-segmented anterior pleopod. MCCM-LH 13623: Habitus of specimen in dorsal aspect. MCCM-LH 15133a: Specimen in lateral aspect showing proximal part of pereipods and pleopods. MCCM-LH 17190b: Specimen in lateral aspect exposing proximal part of posterior pereipods and pleopods.

FIG. 2. *Spinogriphus ibericus* gen. et sp. nov., Upper Barremian, Las Hoyas, Central Spain. A, specimen LH-2195b (paratype) in dorsal aspect showing body tagmosis, posterolateral extensions of carapace, and proximal part of uropods. B, specimens LH-2194b (paratypes) in lateral and dorsal aspect, respectively, showing same body features as A. C, specimen LH-8144a (paratype) in dorsolateral aspect showing body tagmosis, antennules and antennae, pereipods, vestiges of pleopods, uropods and telson. All light photographs with image colour inverted to blue then converted to grayscale.



Diagnosis. As for the genus.

Derivation of name. The species name refers to the Iberian Peninsula, region where the new taxon was discovered.

Description

Body length. Ranging between 6.6 and 10.8 mm (n = 6); all measured specimens adult; sexual dimorphism not detected.

Cephalothorax. The animal has a short, rounded dorsal cephalothoracic shield that covers entirely the first pereionite (Fig. 2A, C) and extends posterolaterally to partially cover the lateral surfaces of the second pereionite (Figs 2B and 3C; also visible in specimen MCCM-LH 13623, not figured); it does not cover the mouthparts, which appear fully exposed laterally (Fig. 2B). The posterodistal angles of these carapace extensions are evenly rounded (Fig. 2B, C). In contrast to the condition evident in Recent spelaeogriphaceans, no clear trace of notch separating the lateral from the dorsal part can be discerned on the anterolateral margin of the cephalothoracic shield. Similarly, no rostrum, cervical furrow or eyestalks appear outlined in any of the preserved specimens; however, the eyestalks and the cervical furrow are extremely faint in some Recent spelaeogriphaceans (Gordon 1957, pp. 32–33). Therefore, the presence of these structures in the new fossil cannot be conclusively excluded. Nothing remarkable can be said about the mouthparts except that they seem to be ordinarily developed (Figs 2B and 3A, B).

The antennule comprises a three-segmented peduncle (Figs 2C, 4A and 5F; also visible in specimen LH-17349a, not figured), with the more distal segments progressively shorter; in dorsal aspect, the proximal segment is subrectangular, the other two are subquadrate (Fig. 5F; also visible in specimen LH-17349a, not figured). There are two terminal, multi-annulate flagella carried on the distal segment of the peduncle (Fig. 4A; hardly visible in both antennular branches in Fig. 4C; also in Fig. 2C).

The antenna is biramous (Fig. 4D). The peduncle is apparently three-segmented, with the protopodal part short, broad and apparently unsegmented (Figs 2C and 4D). The exopod is ellipsoidal, scale-like, and as long as the proximal endopodal segment (Figs 4C, D and 5F). The endopod comprises at least two elongate segments proximally plus a long, multiannulate flagellum (Figs 4A, C, D and 5F). Modern spelaeogriphaceans display a five-segmented peduncle on the antenna, comprising two protopodal and three endopodal segments, with the most proximal endopodal segment being extremely short and hardly visible (Poore and Humphreys 2003); this reduced segment could not be discerned in the fossil, but could easily have been obscured.

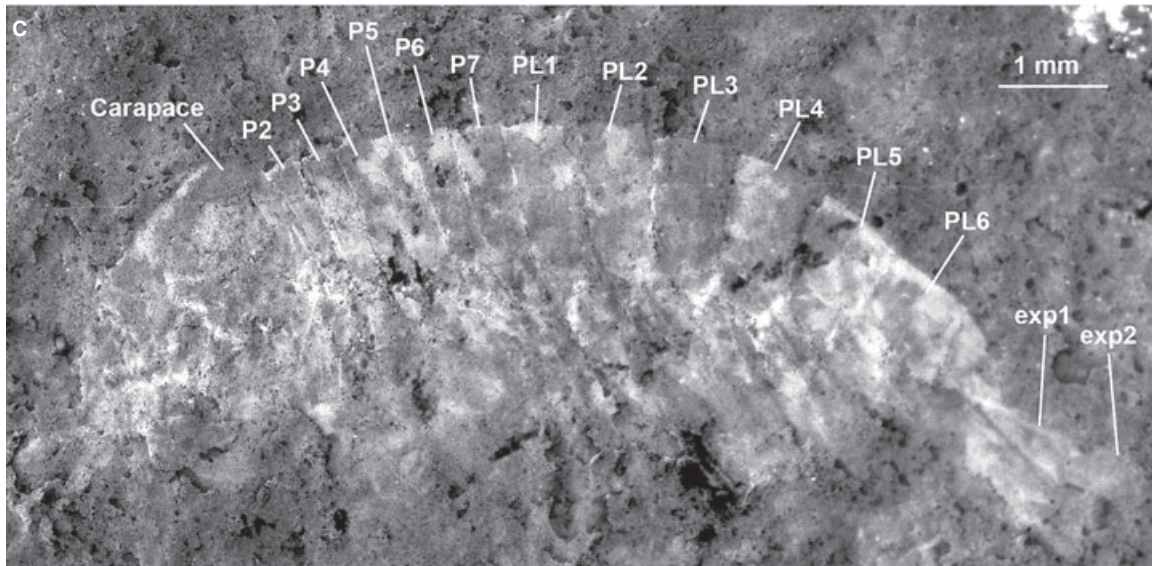
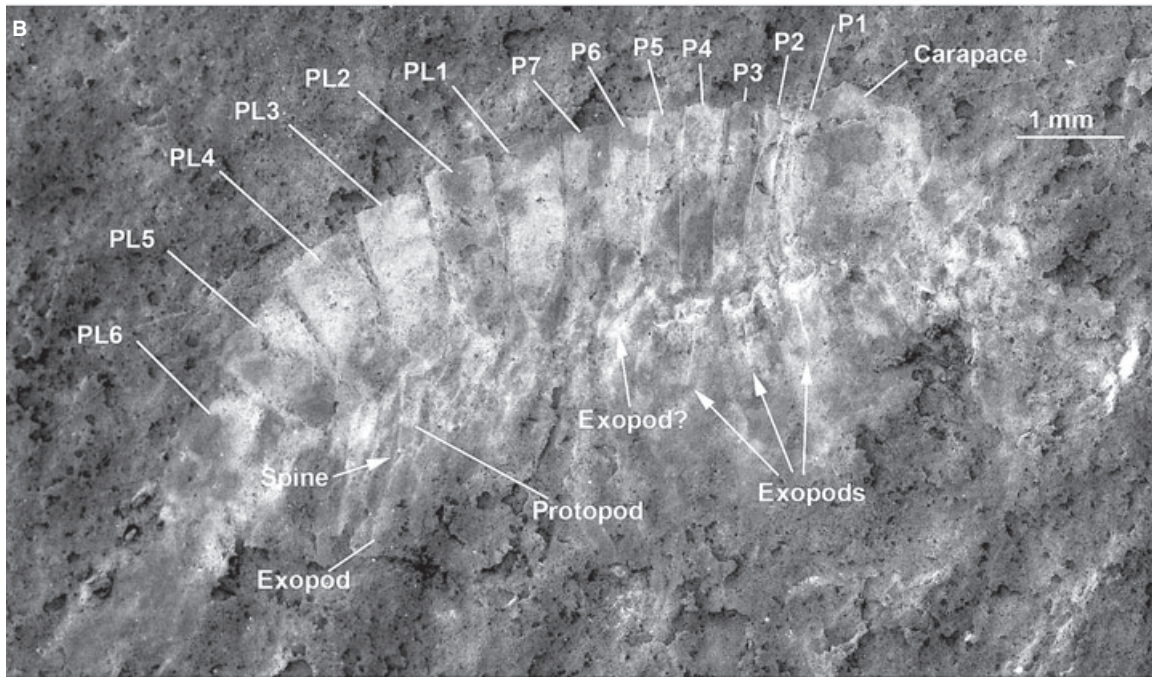
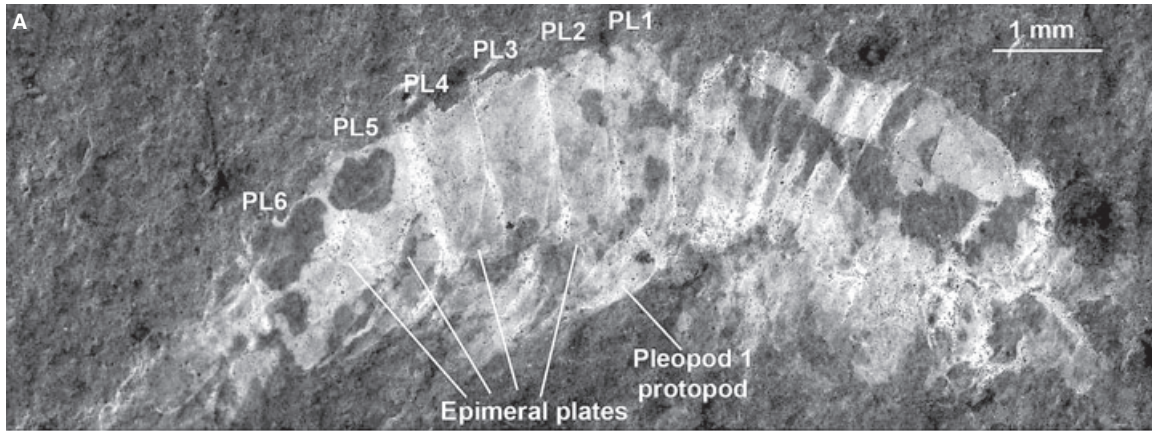
The two segments of the endopod of the new taxon, although subequal in length, differ in width, the first segment being remarkably stouter than the second (Fig. 4A, C, D). The flagellum is sharply flexed at the base, apparently because it inserts subdistally on the distal endopodal segment: the flagellum is therefore reflexed so it is directed postero-laterally to almost posteriorly (parallel with the long axis of the body; Fig. 4A, D).

Pereion. The pereion comprises at least six free exposed pereionites (Figs 2A, B, 3C and 5D, F, visible also in specimen LH-13536, not figured). Some specimens in which the carapace is stretched, folded or lost, expose a presumed free pereionite 1 (Figs 2C, 3B and 4E), which remains concealed beneath the carapace in nonstretched specimens. Pereionites 2–5 are similar in length and clearly shorter than pereionite 6, the latter is clearly shorter than pereionite 7 (see specimen in lateral aspect in Fig. 2B; visible also in specimen LH-1784b, not figured).

Seven stenopodial pereiopods, each provided with an elongate basis, are visible on the right side of Figure 5A; all look structurally similar, with no conspicuous modifications apparent on the more anterior ones (Figs 2C and 5A). Specimen LH-17349a shows the internal foramen of the coxa of the right pereiopod 1 where it articulates with the body, as viewed dorsally through the corresponding body tergite (Fig. 5A). This presumed coxa displays a deep invagination on the lateral side (Fig. 5B) that could correspond to the typical peracarid coxo-basal condyle (Hessler 1982). Traces of a presumed short exopod or epipod (there is no way to resolve whether they originate on the coxa (=epipod) or on the proximal portion of the basis (=exopod) of the corresponding limb) can be discerned on at least pereiopods 1, 3 and 4 in Figure 3B, and in several anterior pereiopods in Figure 2C; all them are about as long as the corresponding basis, and none shows traces of segmentation or armature; that on pereiopod 3 of Figure 3B seems to be tapering and could correspond to the section of a foliaceous unarmed exopod or epipod. It is worth mentioning here that in modern spelaeogriphaceans (which lack epipods on pereiopods), the exopods of the anterior pereiopods are slender, two-segmented and provided with long setae; only the rear pereiopods display a transformed exopod in the form of a foliaceous gill. The presence of branchial exopods on the rear pereiopods of the taxon from Las Hoyas, which would be diagnostic of a spelaeogriphacean, cannot be confirmed.

Pleon. The pleon comprises six free pleonites plus a free articulated telson. The pleonites are subrectangular in dorsal aspect and about equal in length except pleonite 6, which is clearly longer than rest (Figs 2A–C, 3B, C, 4E and 5D, F; also visible in specimens LH-13536 and LH-13623, not figured). Posteroventrally produced epimeral plates are visible on pleonites 1–5 (Fig. 3A).

FIG. 3. *Spinogriphus ibericus* gen. et sp. nov., Upper Barremian, Las Hoyas, Central Spain. A, specimen LH-15083a (paratype) in lateral aspect showing pleon tagmosis, traces of epimeral plates and broad protopod of pleopods. B, specimen LH-16042a (holotype) in lateral aspect showing body tagmosis, traces of presumed pereiopodal exopods, relative proportions of pleopod protopod and exopod, and presumed spine on distolateral angle of protopod of pleopod; note first pereionite exposed beside stretched carapace. C, specimen LH-16042b (paratype) in lateral aspect showing body tagmosis and two-segmented condition of exopod of uropods. All light photographs with image colour inverted to blue then converted to grayscale.



Pleopods are present on all pleonites, and none appears reduced in size. They comprise a broad unsegmented protopod (Figs 3A and 5C) and apparently ovoid, foliaceous rami (Fig. 3B, C; pleopods also discernible in specimens LH-13531 and LH-13536, not figured). The protopod carries a short spine at the distolateral angle (Figs 3B and 5E). The exopod is of a similar length to, or slightly longer than, the protopod (Fig. 3B). The endopod cannot be outlined with precision in any of the available specimens (Fig. 3C).

The uropods together with the telson form a tail fan-like terminal structure. The uropodal protopod is subquadrate and apparently smooth, each articulating ventrolaterally with the sixth pleonite (Figs 2A, B and 5D); the protopod is shorter than both the sixth pleonite itself and the proximal exopodal segment of uropod (Figs 2B and 5F). The exopod is foliaceous and two-segmented (Figs 3C and 5F), with the proximal segment expanded distally (Figs 2B and 5E) and with its medial and distal margins fringed with long (as long as segment width) and stout spines (Figs 4B and 5E); there is at least one stout spine at the distolateral angle of the segment (Figs 2C and 5E; visible also in specimen LH-17349a, not figured). The distal segment is spatulate and shorter than its proximal counterpart (Figs 3C and 5F). Traces of a presumed narrow endopod of about same length as the proximal exopodal segment appear visible in Figs 4B and 5F.

The telson is subtriangular, slightly longer than the uropodal protopod and provided with long and stout spines (clearly more than half as long as telson) at least along the distal and distolateral margins (Figs 2C and 4F).

Digestive system. Several parts of the gut tract, full of amorphous material, are exposed in some specimens (Fig. 4E; visible also in specimen LH-13221a). It is a linear tube with the anterior portion (stomach?) apparently more voluminous than the slender midgut.

Distribution. Restricted to the Upper Barremian lacustrine layers of Las Hoyas site (Southwestern Iberian Ranges, La Huérguina Formation; Central Spain).

Remarks. *Spinogriphus ibericus* gen. et sp. nov. differs from all living spelaeogriphaceans in the possession of a cephalothoracic shield lacking a notch on the anterolateral margin separating the lateral parts from the dorsal part (Figs 2A and 6). The presence of a row of stout spines along the distal margin of the proximal segment of the uropodal exopod along the inter-segmental articulation is also remarkable (Figs 4E and 6). No modern spelaeogriphaceans carry spines in such a position, and they are present only along the medial margin and on the distolat-

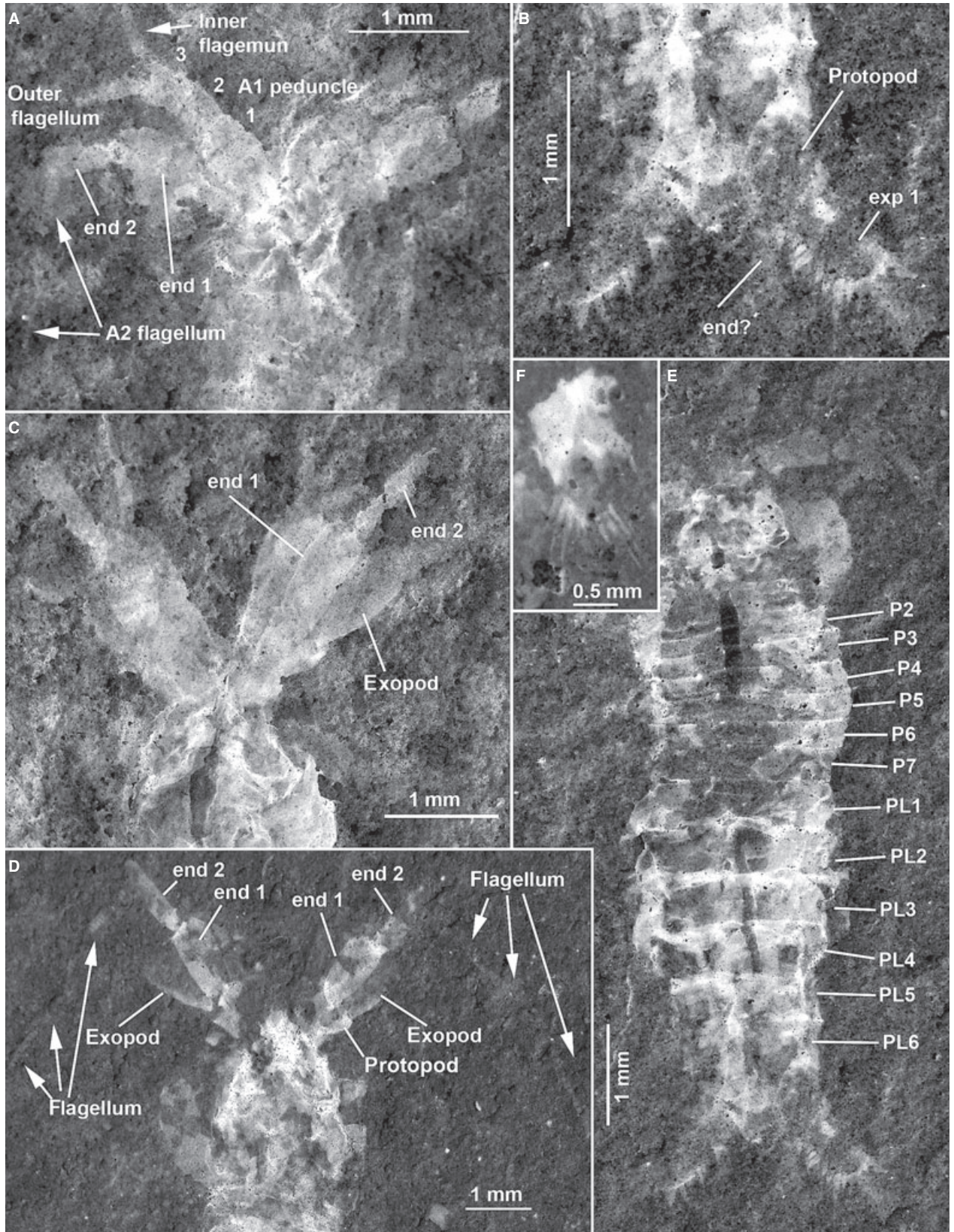
eral angle of the segment. In addition, the two endopodal segments of the antenna of the new taxon are equal in length, and the flagellum is reflexed (Figs 4D and 6); in the two species of *Mangkurtu* (Poore and Humphreys 1998, fig. 4a; 2003, fig. 1c) and in *Potiicoara* (Pires 1987, fig. 6), the proximal segment of the antennal endopod is clearly shorter than the distal segment, and the reverse holds for *Spelaeogriphus* (Gordon 1957, figs 2, 3). The spines present along the distal and distolateral margins of the telson are well developed, equal to half the telson length, and are comparatively much more elongate in the new taxon than in any other spelaeogriphacean. Additional differences from *Spelaeogriphus lepidops* pertain to the reduced antennal exopod and pleopod 5 displayed by this South African taxon (Gordon 1957). The absence of eyestalks in *Spinogriphus* gen. nov., if confirmed, would be another significant difference from modern spelaeogriphaceans.

Comparison of *Spinogriphus* gen. nov. with the two fossil forms currently considered to be spelaeogriphaceans reveals several differences. *Spinogriphus* gen. nov. differs from *Acadiocaris* in the much shorter telson (about as long as the uropodal protopod vs. clearly longer than this segment in *Acadiocaris*) and a presumably shorter uropodal endopod (vs. uropodal rami almost equal in length in *Acadiocaris*; compare Figs 4B and 5D with Schram 1974, figs 15b, c). In addition, the telson spines are much longer in *Spinogriphus* (Fig. 4F). Another remarkable difference between these taxa involves the antennal flagellum, which seems not to be geniculate in *Acadiocaris* (compare Fig. 4D with Schram 1974, fig. 11a, b). *Liaoningogriphus* from China differs from the new taxon in its weakly armoured telson (see Shen *et al.* 1998, plate IIa). In addition, this taxon seems to display a nongeniculate antennal flagellum, although this feature does not appear fully resolved in Shen *et al.* (1998, fig. 2a, c). Conversely, the peculiar 'bipartite' exopods of the pleopods of *Liaoningogriphus* contrast with the apparently normal, unsegmented rami of *Spinogriphus* gen. nov. although, again, the poor preservation of specimens does not allow more detailed comparison.

DISCUSSION

Even though the crustacean from Las Hoyas does not display the diagnostic peracarid female brood pouch, other

FIG. 4. *Spinogriphus ibericus* gen. et sp. nov., Upper Barremian, Las Hoyas, Central Spain. A, specimen LH-13531 (paratype) in dorsal aspect, inset of left antennule and antenna. B, specimen LH-15298 (paratype) in dorsal aspect, inset of uropods. C, specimen LH-7302a (paratype) showing antennal segmentation. D, specimen LH-1979 (paratype) in dorsal aspect, inset of head with exposed antennae; notice geniculate antennal flagella. E, specimen LH-15298 (paratype) in dorsal aspect showing body somites; note exposed pereonite 1 beside stretched carapace. F, specimen LH-26953a (paratype), inset of telson. All light photographs with image colour inverted to blue then converted to grayscale.



features suggest that it should be considered as a member of the Peracarida. Thus, in contrast to syncarids, it has a short carapace (= posterior extension of the cephalothoracic shield), and the bases of the pereopods are elongate (vs. short in syncarids). In addition, the coxa-basis articulation of the pereopods is apparently monocondylic (i.e. with single invaginated condyle); this is the typical condition found in most peracarids including modern spelaeogriphaceans and contrasts with the dicondylic articulation present in syncarids (see Hessler 1982).

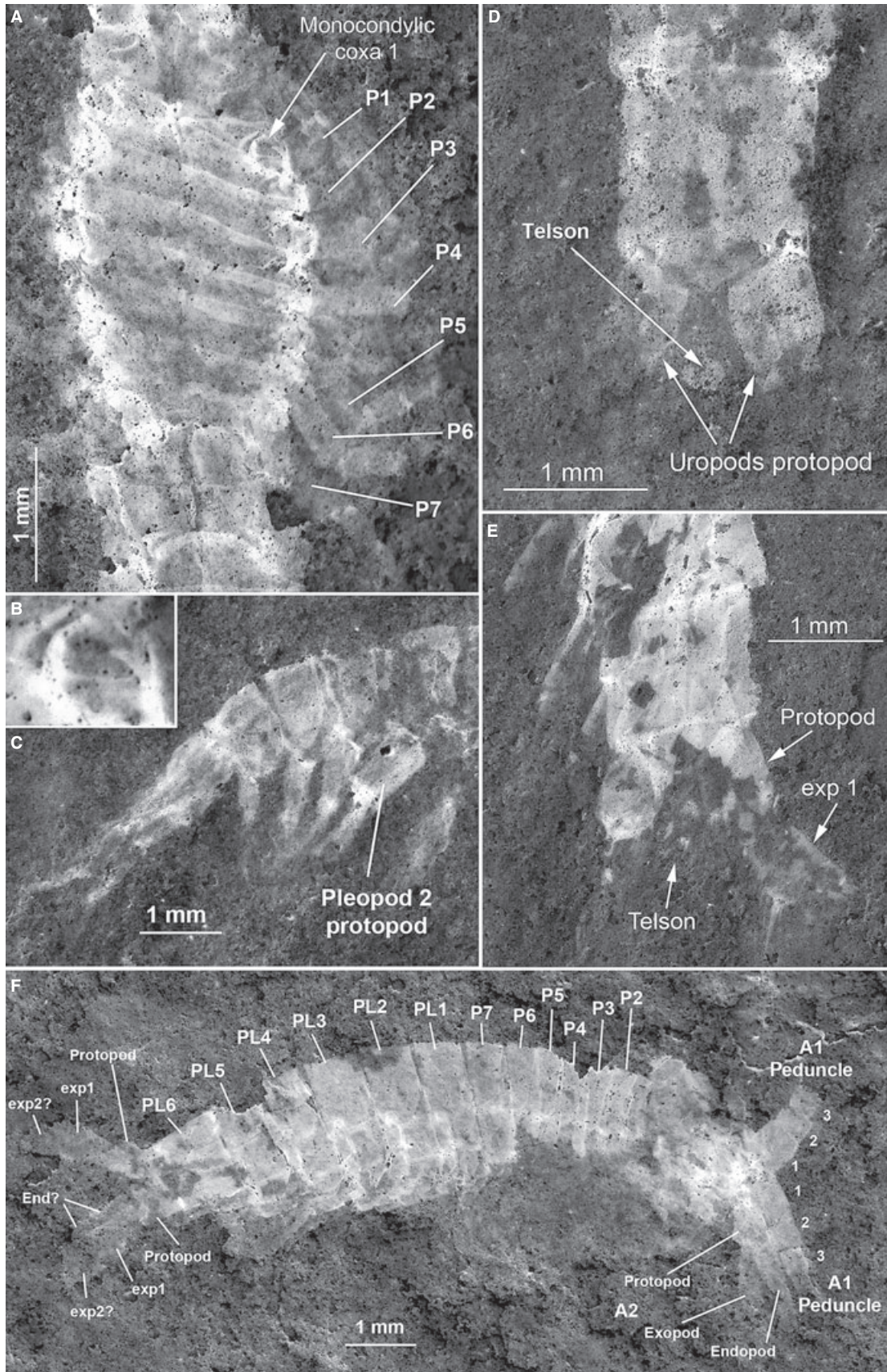
The general features of the cephalothorax of the new taxon conform to those of a modern spelaeogriphacean: There is a short carapace covering only the first pereonite, and none of the pereonites appears incorporated into the cephalothorax. The presumed absence of eyestalks in the new fossil form, if confirmed, cannot be considered as a character of significance at the ordinal level because other well-defined peracarid orders such as the Thermosbaenacea include taxa with developed eyestalks (e.g. Tulumellidae and Halosbaenidae) and taxa devoid of them (e.g. Monodellidae and Thermosbaenidae; see Wagner 1994). It is worth mentioning here also that some thermosbaenaceans, for example males and nonovigerous females of *Monodella* Ruffo, 1949, *Tethysbaena* Wagner, 1994, *Halosbaena* Stock, 1976 and *Theosbaena* Cals and Boutin, 1985, share with spelaeogriphaceans the possession of a short posterolateral extension of the cephalothorax that extends only over the first pereonite (Fryer 1964; Wagner 1994; Shimomura and Fujita 2009).

The general features of the trunk of the new taxon conform to those of a generalised peracaridan, distinguished mostly by the lack of the apomorphies characteristic for each of the major peracaridan taxa (see Poore 2005). The combination of the apparent absence of modifications of the anterior pereopods, the free condition of the anterior pereonites (i.e. none appears incorporated into the cephalothorax), and the presence of a short carapace exhibited by the new taxon is shared with the spelaeogriphaceans and with male or nonovigerous female thermosbaenaceans. Affinities with the Mictacea can be eliminated because of the absence of a carapace in this group and because of additional differences in characters relating to the pleopods and the uropods. Unfortunately, the unresolved state of the pereopodal exopods of the fossil prevents us from unequivocally confirming its spelaeogriphacean affinities.

The pleon of the fossil taxon resembles that of a spelaeogriphacean in all respects. The features of other generalised peracarids do not fit the pattern of the fossil. Thus, *Mictocaris* Bowman and Iliffe, 1985 (Mictacea) and all members of the Thermosbaenacea have vestigial pleopods in sharp contrast with the well-developed foliaceous pleopods present on all pleonites of the new taxon (Bowman and Iliffe 1985; Wagner 1994). In addition, *Mictocaris* displays a long two-articulate uropodal endopod. Some peracarids, such as bochusaceans and some tanaids and cumaceans, show a multi-articulated (but unsegmented; see Jaume *et al.* 2006) uropodal endopod. This is not the case in spelaeogriphaceans or thermosbaenaceans, both of which display an unsegmented endopod lacking annulation. Male bochusaceans approach the spelaeogriphacean condition in displaying well-developed pleopods provided with a robust protopod on all pleonites, but here both rami are slender and annulated, not foliaceous. In addition, the telson in bochusaceans is incorporated into the sixth pleonite to form a pleotelson, whereas in spelaeogriphaceans the telson is free. Nevertheless, as in the case of eyestalks, this feature should not be considered as diagnostic at the ordinal level because some thermosbaenaceans (e.g. *Thermosbaena* Monod, 1924) have a pleotelson, whereas the other members of the order have the telson separated from the sixth pleonite (Wagner 1994).

Modern spelaeogriphaceans, thermosbaenaceans and mictaceans – the three peracaridan orders the new taxon from Las Hoyas could be related to – all show a relict distribution restricted to subterranean waters. In contrast, the Upper Jurassic fossil *Liaoningogriphus* from China, although apparently devoid of eyes, was an epigeal lacustrine form that lived in a nonkarstic lake developed on basaltic rock (Shen *et al.* 1998). Because of the nature of its geological setting, connection of this lacustrine habitat to the groundwater environment seems improbable, raising the possibility that the presence of *Liaoningogriphus* in the lake was accidental, and that the primary habitat of this taxon corresponds to the ground water table. Stygobiont crustaceans (= obligate dwellers in subterranean waters) are rarely reported from lake bottoms, and such reports usually consist of interstitial forms showing the typical body modifications, that is, they have a vermiform aspect and short appendages. These specimens are always found in dredged sand or gravel coarse enough as to

FIG. 5. *Spinogriphus ibericus* gen. et sp. nov., Upper Barremian, Las Hoyas, Central Spain. A, specimen LH-17349a (paratype) in dorsal aspect, inset of pereion; note elongate basis of pereopods and presumed monocondylic coxa-basis articulation on pereopod 1. B, detail of latter. C, specimen LH-17054 (paratype) in lateral aspect, inset of pleon showing expanded protopod of pleopods. D, specimen LH-1784b (paratype) in ventral aspect, inset of pleonite 6 with protopod of uropods attached. E, specimen LH-26953b (paratype) in ventral aspect showing armature on uropods and telson. F, specimen LH-21253a (paratype) in dorsal aspect showing body tagmosis and segmentation of antennules, antennae and uropods. All light photographs with image colour inverted to blue then converted to grayscale.



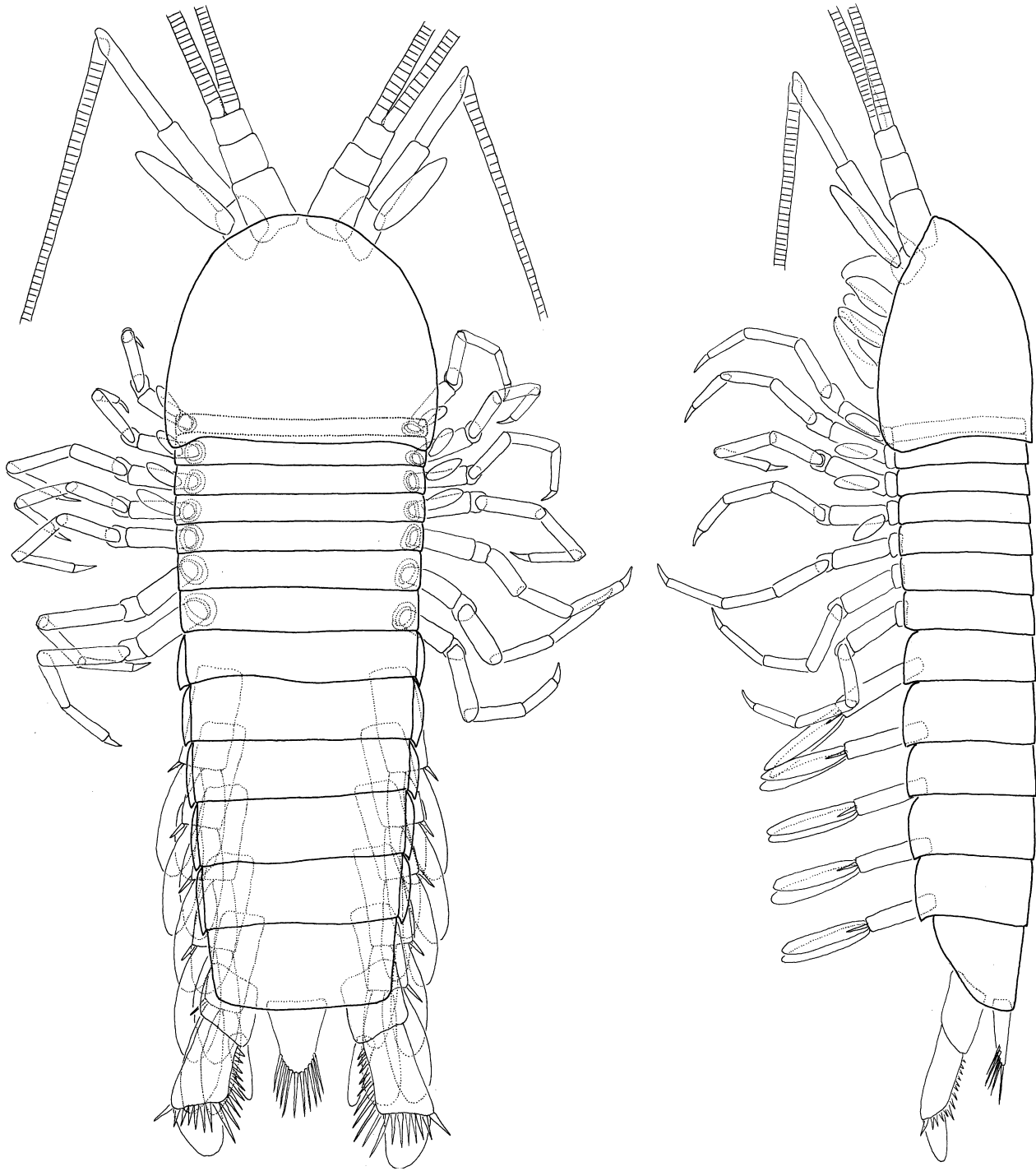


FIG. 6. Reconstruction of *Spinogriphus ibericus* gen. et sp. nov., in both dorsal and lateral aspects. Note that pereiopodal exopods have been tentatively represented as nonsetose respiratory paddles as in modern spelaegriphaceans.

allow the establishment of an interstitial fauna. They are not found in fine-grained shales similar to those rendering the fossil spelaegriphaceans. This holds for the two endemic bathynellaceans of Lake Baikal, living between 20 and 1440 m depth (Bazikalova 1954; Birstein and Ljovuschkin 1967), and also for a population of the

cave-dwelling *Iberobathynella magna* Camacho and Serban, 1998 discovered under a 90-m-depth water column in a Spanish reservoir (Arbón, Asturias; D. J., pers. obs.; Camacho 2003). However, the morphology of modern spelaegriphaceans and of *Liaoningogriphus*, as well as the epibenthic or nectonic habits of the former (Gordon

1957; Hessler 1982; Pires 1987), is not in accord with an interstitial life-style. Uncertainty remains concerning the precise habitat of the Carboniferous *Acadiocaris* from Canada, as discussed above, although it was probably limnic.

Spinogriphus gen. nov. was undoubtedly a freshwater form. The specimens appear within laminites and are largely intact from which we infer that the source of the population was not far from the place of burial. However, this cannot be considered compelling evidence that the main habitat of the species was the water column or the epibenthos. Because the rock underlying the lake sediments is strongly karstified (Fregenal-Martínez and Melendez 2000), and there is geochemical evidence pointing to the lake receiving groundwater (Poyato-Ariza *et al.* 1998), the question arises whether the crustaceans could have been outwashed into the lake from a subaquatic spring or groundwater seep. The fossil crustaceans occur mixed with thousands of fragments of charophytes; these green algae need sunlight to photosynthesise, but are often found in calcareous springs.

It is possible that the fossils could be stygobionts established in subaquatic springs or groundwater seeps even if the main habitat of the species was the groundwater table, from where they could periodically be carried into the lake during episodes of strong groundwater discharge. The animals currently found within the laminites would correspond to such displaced specimens that had been advected into the lake basin. Botosaneanu (1998) lists numerous cases of permanent populations of troglomorphic crustaceans (i.e. displaying morphological features typical of subterranean animals, such as the absence of eyes) inhabiting such habitats (the so-called 'crenobionts'). Wilson and Ponder (1992), for example, found eyeless phreatoicid isopods of the genus *Tainisopus*, living downstream from their home springs in Western Australia.

If *Spinogriphus* gen. nov. were a true stygobiont, it would be the second oldest known. The oldest appears to be the marine thaumatocypridid ostracod *Pokornyopsis feifeli* Triebel, 1941, known from Late Jurassic (Callovian to Oxfordian) tensional vertical and horizontal fissures (the latter interpreted as submarine caves) in the Czorsztyn Unit, Western Carpathians, Slovakia (Aubrecht and Kozur 1995). However, the mass occurrence of ostracod remains in these fissures (1000–10 000 specimens per kg of sediment; Aubrecht and Kozur 1995, p. 7) is not in accord with the extremely low densities of organisms found in modern anchialine caves. In addition, their presence in the interspaces of contemporaneous limestone breccias suggests that the habitat of this species was not restricted to these presumed caves but included also the crevicular marine habitat.

Acknowledgements. This is a contribution to Spanish MICINN projects CGL 2009-11838 BTE and CGL2009-08256, the latter in part co-financed with EU FEDER funds. We are indebted to Angela D. Buscalioni for the invitation to work on this material. Work at Las Hoyas is recurrently funded and supported by Consejería de Educación, Ciencia y Cultura, Junta de Castilla-La Mancha. Fernando Escaso, curator of the collection of fossils at Museo de las Ciencias de Castilla-La Mancha, is gratefully acknowledged for the facilities provided to study the specimens. We are grateful to Anna Iglukowska for preparing Figure 1.

Editor. Jason Dunlop

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