

# 11.9 Spelaeogrifhacea

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**Abstract:** *Spinogrifhus ibericus* is the third fossil attributable to the crustacean peracaridan order Spelaeogrifhacea known to date, and lived in the Upper Barremian Las Hoyas lacustrine site in Central Spain. Neither this taxon nor the other two fossil forms can be identified with certainty as crown-group spelaeogrifhaceans. We consider that Schram's 1974 family Acadiocarididae represents stem-lineage spelaeogrifhaceans and should accommodate these fossil taxa which display very generalised peracaridan features and

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 lacks annulation. The zoogeography of the Acadiocarididae is Laurasian in contrast to the modern, crown-group spelaeogrifhaceans (Spelaeogrifhidae), which are limited to Gondwanan territories.

## Modern Spelaeogrifhaceans

The crustacean order Spelaeogrifhacea 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. *Spelaeogrifhus 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 & 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 Early Cretaceous alluvial conglomerates (Poore & Humphreys 1998, 2003). All these terrains were once part of Gondwana, and we infer that the penetration of spelaeogrifhaceans into continental waters took place prior to the fragmentation of this supercontinent (starting ca. 140 MYA), and that their current distribution pattern reflects plate tectonic history (Pires 1987).

The spelaeogrifhacean body plan is rather featureless at first glance, and this makes the identification of fossils problematic, especially if limbs are not well preserved. Most

spelaeogrifhacean 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 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 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 spelaeogrifhaceans have a ventral marsupium formed by oöstegites (= foliaceous medial processes of the pereopodal coxae – see Boxshall & Jaume 2009).

The most remarkable autapomorphy of the Spelaeogrifhacea is the transformation of the exopods of the posterior pairs of pereopods into non-setose, respiratory paddles (Grindley & Hessler 1971, Richter & Scholtz 2001). Another characteristic of the group is the short, posteriorly-directed carapace formed as an extension of the rear margin of the dorsal cephalothoracic shield and concealing part of the first pereionite.

## The presumed Spelaeogrifhacean of Las Hoyas

The Las Hoyas specimens (Plate 1) were originally recognised as a spelaeogrifhacean, but not published, by Pinarido-Moya, and formally described by Jaume et al. (*in press*) as a new genus and species *Spinogrifhus ibericus*. This taxon is based on 25 specimens corresponding to the best-preserved individuals collected in the field. Most of them are preserved either in dorsal or in lateral aspect. Portions of the gut tract, full of amorphous material, are exposed in some specimens. Body length ranges between 6.6 and 10.8 mm. The genus name refers to the telson, which is provided with long, stout spines. The animal has a short, rounded dorsal cephalothoracic shield that covers entirely the first pereionite and extends posterolaterally to partially cover the lateral surfaces of the second pereionite; it does not cover the mouthparts, which appear fully exposed laterally. In contrast to the condition evident in Recent

spelaeogrifhaceans, no clear trace of a 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 spelaeogrifhaceans (Gordon 1957: 32–33). Therefore the presence of these structures in the new fossil cannot be definitively excluded.

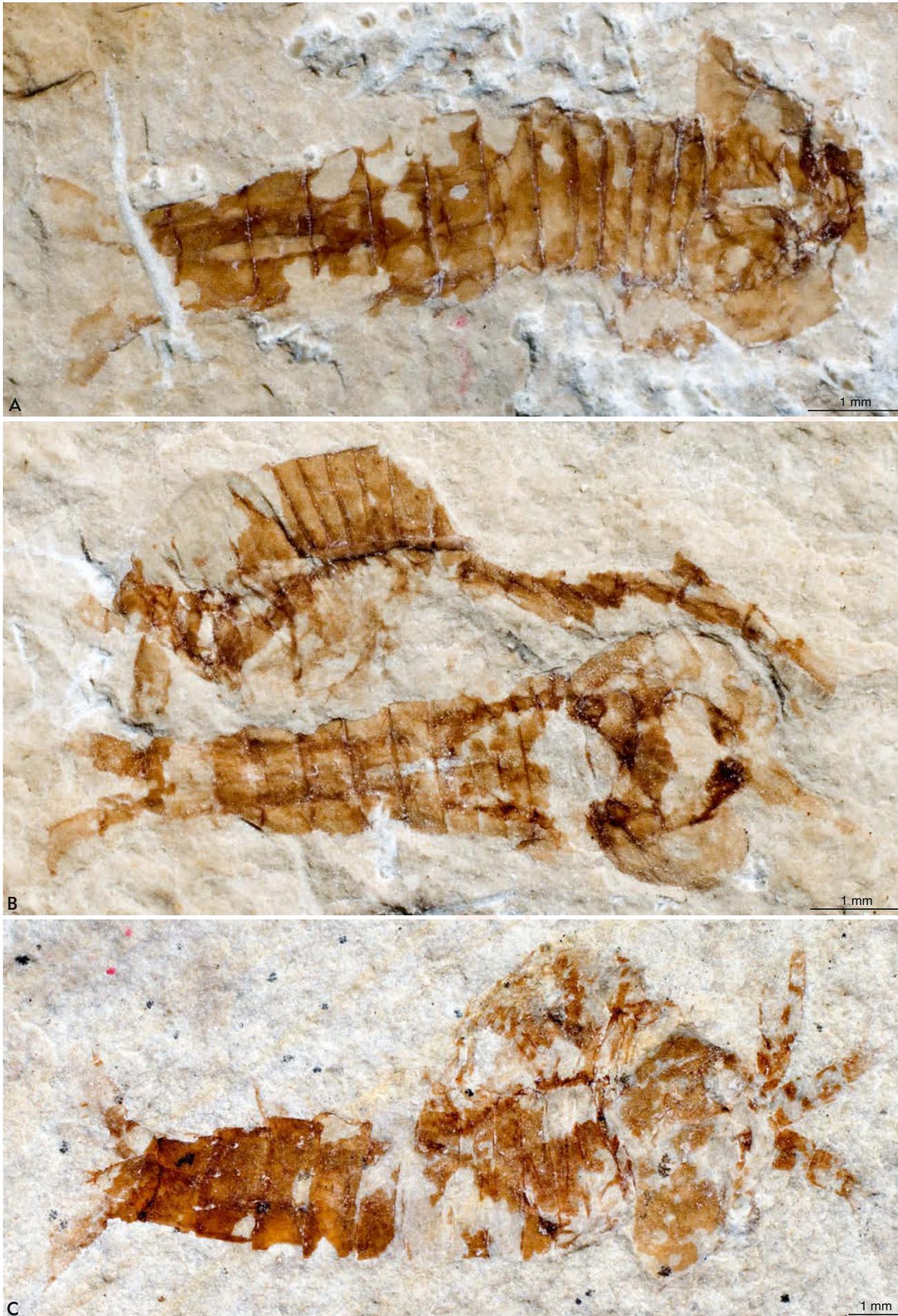
The antennule comprises a three-segmented peduncle, with the more distal segments progressively shorter; in dorsal aspect the proximal segment is subrectangular, the other two are subquadrate. There are two terminal, multi-annulate flagella carried on the distal segment of the peduncle.

The antenna is biramous. The peduncle is apparently three-segmented, with the protopodal part short, broad and apparently unsegmented. The exopod is ellipsoidal, scale-like, and as long as the proximal endopodal segment. The endopod comprises at least two elongate segments proximally plus a long, multiannulate flagellum. Modern spelaeogrifhaceans 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 & 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

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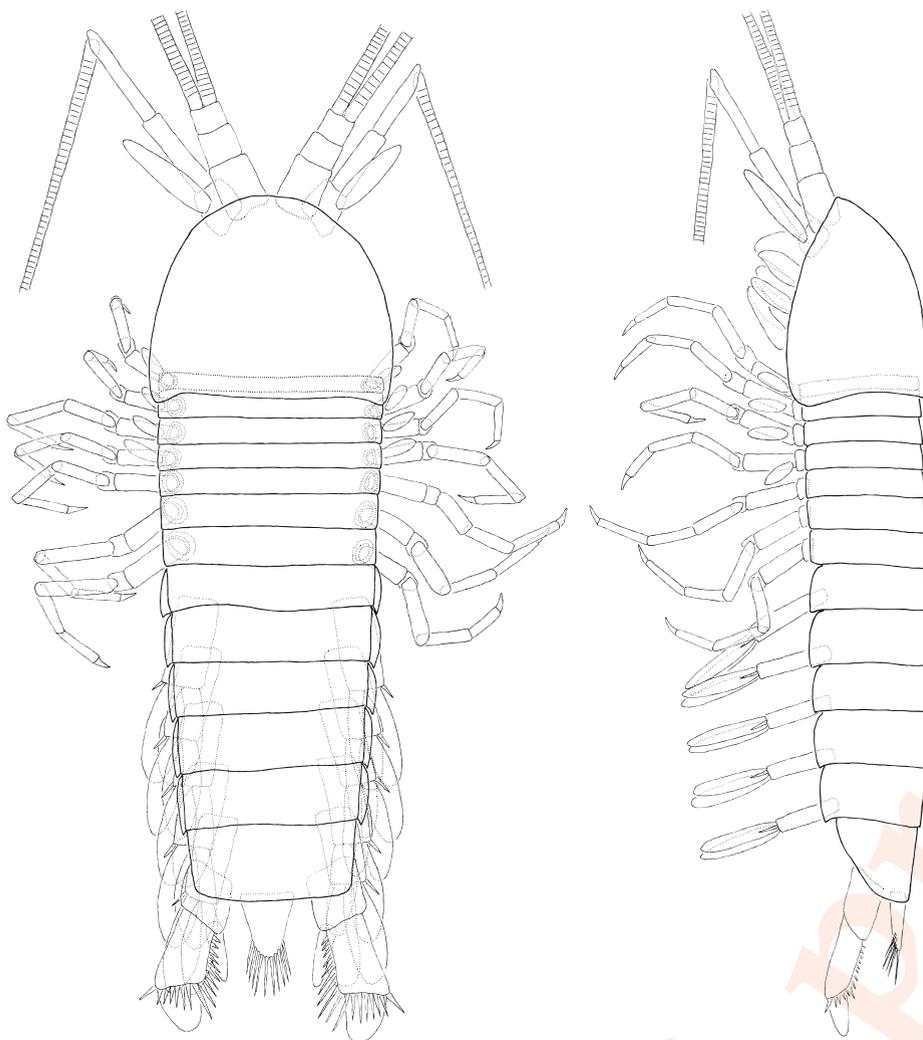
**Plate 1.** *Spinogriffus ibericus* Jaume, Pinaro & Boxshall, 2012 from the upper Barremian of Las Hoyas, Central Spain. **A.** Specimen LH-2195b in dorsal aspect showing body tagmosis, postero-lateral extensions of carapace, and proximal part of uropods. **B.** Specimens LH-2194b in lateral and dorsal aspect, respectively, showing same body features as A. **C.** specimen LH-8144a in dorsolateral aspect showing body tagmosis, antennules and antennae, pereopods, vestiges of pleopods, uropods and telson. Modified from Jaume et al. (2012).

*Spinogriffus*, although subequal in length, differ in width, the first segment being remarkably stouter than the second. 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).

The pereion comprises at least six free exposed pereionites.

Some specimens in which the carapace is stretched, folded or lost, expose a presumed free pereionite 1, which remains concealed beneath the carapace in non-stretched specimens. Pereionites 2–5 are similar in length and clearly shorter than pereionite 6, the latter is clearly shorter than pereionite 7.

Seven stenopodial pereopods, each provided with an elongate basis and all looking structurally similar, with no conspicu-



**Fig. 1.** Reconstruction of *Spinogriphus ibericus* Jaume, Pinardo and Boxshall (in press) in both dorsal and lateral aspects. Pereiopodal exopods have been tentatively represented as non-setose respiratory paddles as in modern spelaeogriphaceans.

ous modifications apparent on the more anterior ones, can be discerned. A presumed coxa displays a deep invagination that

## The relationships of Las Hoyas Spelaeogriphacean

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 tanaiids 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-developed fifth pleopod, than exhibited in the modern family Spelaeogriphidae.

Neither *Spinogriphus* nor the two mentioned fossils 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 which display very generalised peracaridan features but lack any conspicuous autapomorphies except for: a short carapace, undifferentiated pereopods, foliaceous pleopods,

could correspond to the typical peracaridan 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 several anterior pereopods; all them are about as long as the corresponding basis, and none shows traces of segmentation or armature; that on pereopod 3 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 pereopods) the exopods of the anterior pereopods are slender, two-segmented and provided with long setae; only the rear pereopods display a transformed exopod in the form of a foliaceous gill. The presence of branchial exopods on the rear pereopods of the taxon from Las Hoyas, which would be diagnostic of a spelaeogriphacean, cannot be confirmed.

The pleon comprises six free pleonites plus a free articulated telson. The pleonites are about equal in length except pleonite 6, which is subrectangular and clearly longer than rest. Foliaceous pleopods are present on all pleonites, and none appears reduced in size. One of the diagnostic features of the new genus and species is that pleopod 5 is not reduced.

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; the protopod is shorter than both the sixth pleonite itself, and the proximal exopodal segment of uropod. The exopod is foliaceous and two-segmented, with the proximal segment expanded distally and with its medial and distal margins fringed with long (as long as segment width) and stout spines; there is at least one stout spine at the distolateral angle of the segment. The distal segment is spatulate and shorter than its proximal counterpart. Traces of a presumed narrow endopod of about same length as the proximal exopodal segment appear visible in some specimens.

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.

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.

Comparison of *Spinogriphus* with the two fossil forms currently considered to be spelaeogriphaceans reveals several differences. *Spinogriphus* differs from *Acadiocaris* in the much shorter telson and a presumably shorter uropodal endopod. In addition, the telson spines are much longer in *Spinogriphus*. Another remarkable difference between these taxa involves the antennal flagellum, which seems not to be geniculate in *Acadiocaris*. *Liaoningogriphus* from China differs from the Las Hoyas taxon in its weakly armoured telson. In addition, *Liaoningogriphus* seems to display a non-geniculate antennal flagellum, although this feature does not appear fully resolved in Shen et al. (1998: fig. 32a,c). Conversely, the peculiar "bipartite" exopods of the pleopods of *Liaoningogriphus* contrast with the apparently normal, unsegmented rami of *Spinogriphus* although, again, the poor preservation of specimens does not allow more detailed comparison.

*Spinogriphus ibericus* 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. 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. No modern spelaeogriphaceans carry spines in such a position, they are present only along the medial margin and on the distolateral 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; in the two species of *Mangkurtu* (Poore & Humphreys 1998: fig. 34a; 2003: fig. 31c) and in *Potiicoara* (Pires 1987: fig. 36) 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 *Spinogriphus* than in any other spelaeogriphacean.

Additional differences from *Spelaeogriphus lepidops* relate to the reduced antennal exopod and pleopod 5 displayed by this South African taxon (Gordon 1957). The absence of eyestalks in *Spinogriphus*, if confirmed, would be another significant difference from modern spelaeogriphaceans.

## Lifestyle and ecology

*Spinogriphus* was undoubtedly a freshwater form (Fig. 1). 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. Since the rock underlying the lake sediments is strongly karstified (Fregenal-Martínez & Meléndez 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 & Ponder (1992), for example, found eyeless phreatoicid isopods living downstream from their home springs in Western Australia.

If *Spinogriphus* were a true stygobiont, it would be the second oldest known. The oldest appears to be the marine thaumatocyprid 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 & Kozur 1995). However, the mass occurrence of ostracod remains in these fissures (1000 to 10000 specimens per kg of sediment; Aubrecht & Kozur 1995: 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.

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