

Skeletonized microfossils from the Lower–Middle Cambrian transition of the Cantabrian Mountains, northern Spain

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Two different assemblages of skeletonized microfossils are recorded in bioclastic shoals that cross the Lower–Middle Cambrian boundary in the Esla nappe, Cantabrian Mountains. The uppermost Lower Cambrian sedimentary rocks represent a ramp with ooid-bioclastic shoals that allowed development of protected archaeocyathan-microbial reefs. The shoals yield abundant debris of tube-shelled microfossils, such as hyoliths and hyolithelminths (*Torelrella*), and trilobites. The overlying erosive unconformity marks the disappearance of archaeocyaths and the Iberian Lower–Middle Cambrian boundary. A different assemblage occurs in the overlying glauconitic limestone associated with development of widespread low-relief bioclastic shoals. Their lowermost part is rich in hyoliths, hexactinellid, and heteractinid sponge spicules (*Eiffelia*), cancelloriid sclerites (at least six form species of *Allonnia*, *Archiasterella*, and *Chancelloria*), cambroclaves (*Parazhijinites*), probable eoconchariids (*Cantabria labyrinthica* gen. et sp. nov.), sclerites of uncertain affinity (*Holoplicatella margarita* gen. et sp. nov.), echinoderm ossicles and trilobites. Although both bioclastic shoal complexes represent similar high-energy conditions, the unconformity at the Lower–Middle Cambrian boundary marks a drastic replacement of microfossil assemblages. This change may represent a real community replacement from hyolithelminth-phosphatic tubular shells to CES (cancelloriid-echinoderm-sponge) meadows. This replacement coincides with the immigration event based on trilobites previously reported across the boundary, although the partial information available from originally carbonate skeletons is also affected by taphonomic bias.

Key words: Skeletonized microfossils, cambroclavids, cancelloriids, hyoliths, hyolithelminths, sponges, benthic replacement, Cambrian, Cantabrian Mountains, Spain.

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Introduction

The Lower–Middle Cambrian transition, in its regional Mediterranean sense (see recent summary in Álvaro and Clausen 2005), is a key interval for testing the relationship between the stratigraphic completeness of the fossil record and the benthic community replacements recorded in different parts of the western Gondwana margin. This time span was rich in paleogeographic and paleoecological events in West Gondwana, such as the stepwise decrease in carbonate productivity, the abrupt disappearance of their associated microbial and archaeocyathan-microbial reef ecosystems, the record of an episodic tectonic instability correlatable across different platforms, and a drastic change to open-sea conditions that favored the appearance of a relatively cosmopolitan trilobite fauna (see recent summaries in Álvaro et al. 2000a, 2003; Álvaro and Vennin 2001). However, each platform recorded different benthic community replacements as a consequence

of their particular paleoecological and environmental conditions (Álvaro et al. 1999, 2003; Álvaro and Clausen in press).

The Lower–Middle Cambrian boundary, defined in the Iberian Peninsula by the lowest appearance of the trilobite *Acadoparadoxides mureoensis* (Sdzuy, 1958), is linked in the Iberian Chains (NE Spain) with the Valdemiedes event, a synchronous change in fauna related to a stepwise immigration of relatively cosmopolitan invaders (Álvaro et al. 1999). At present day, the stratigraphic successions in which this event is recognized lie exclusively in the Iberian Chains. The occurrence of *A. mureoensis* in the Cantabrian Mountains was reported by Álvaro et al. (1993) in the Esla nappe, a region recently analyzed from sedimentologic and sequence stratigraphic viewpoints (Álvaro et al. 2000b). The importance of the Lower–Middle Cambrian transition in the Esla nappe is related to two distinct paleogeographic patterns: the occurrence of archaeocyathan-microbial buildups (Debrenne and Zamareño 1970; Perejón and Moreno-Eiris 2003) representing the

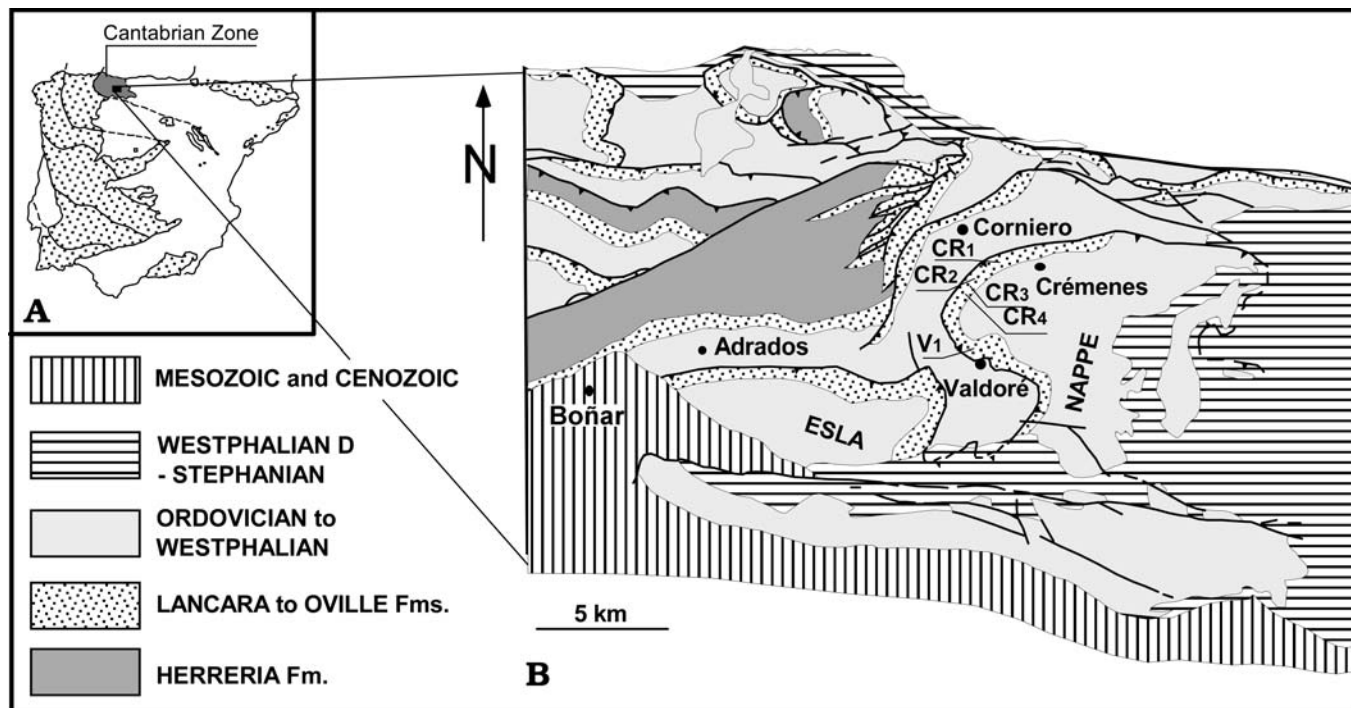


Fig. 1. A. Pre-Hercynian outcrops of the Iberian Peninsula (stippled) and setting of the Esla Nappe in the Cantabrian Zone (grey area). B. Geologic map of the Esla nappe and stratigraphic sections sampled in this work (CR₁₋₄ and V₁; after Truyols et al. 1990; Aramburu et al. 1992; Álvaro et al. 2000b).

youngest Lower Cambrian archaeocyathan zone of the Iberian Peninsula (Moreno-Eiris et al. 1995), and the presence of a regional unconformity within the Lánacara Formation at the Lower–Middle Cambrian boundary (Mohr 1969; Aramburu et al. 1992; Aramburu and García Ramos 1993).

The present work establishes the taxonomic basis of the skeletonized microfossils (“small shelly fossils”) for purposes of paleoecological interpretation of the benthic community replacements recorded across the Lower–Middle Cambrian transition in the Esla nappe. As West Gondwanan skeletonized microfossils are reasonably sparse, the description of these phosphatized microfossils will increase the biogeographic discussions currently based on trilobites (Álvaro et al. 2003).

Institutional abbreviation.—DGO, Faculty of Geology of the Oviedo University, Oviedo, Spain.

Geologic setting and stratigraphy

The fossils described herein occur in the Cantabrian Zone, which is a major tectonostratigraphic unit of the Variscan foreland fold belt located in the northwest of the Iberian Peninsula (Fig. 1). In this area, the Lower–Middle Cambrian transition lies in the Lánacara Formation, which was subdivided by Zamarreño (1972) into two members. The lower member (100–225 m thick) is composed of yellow dolostone, commonly rich in ooids, peloids and stromatolites. In some areas (such as the Esla nappe), the uppermost part of

this member is composed of grey limestone with abundant birdseye fabric and archaeocyathan-microbial reefs (Debrenne and Zamarreño 1970), and ooid-bioclástico limestone (Álvaro et al. 2000b). The base of the Middle Cambrian is located at the base of the upper member (with 1–40 m of global thickness), which consists of grey and pink, ooid-bioclástico limestone rich in glauconite (“Beleño facies”), overlain by an alternation of reddish to purple, nodular limestone and shale that is 0–30 m thick (“griotte” or “Barrios facies” Zamarreño 1972). The unconformity at the Lower–Middle Cambrian boundary in the Esla nappe (Fig. 2), identified at the contact between the two members, is associated with the abrupt disappearance of reef mounds and their associated archaeocyaths and the rapid immigration of diverse, lowermost Middle Cambrian, relatively cosmopolitan trilobites. This hiatus is associated with a basinward facies shift capped by a major unconformity separating sharp changes in the type of carbonate deposition (Álvaro et al. 2000b). Neither C isotope ratios nor best preserved Sr isotope ratios show any major change at the precise level of the boundary that might indicate a significant depositional hiatus (Shields et al. 2004). After a period of erosion, sedimentation continued in a Middle Cambrian transgressive trend in which Lower Cambrian sediments are found as reworked clasts in breccia layers.

Material and methods

The microfossils reported here were found up to 1 m below and above the unconformity at the Iberian Lower–Middle

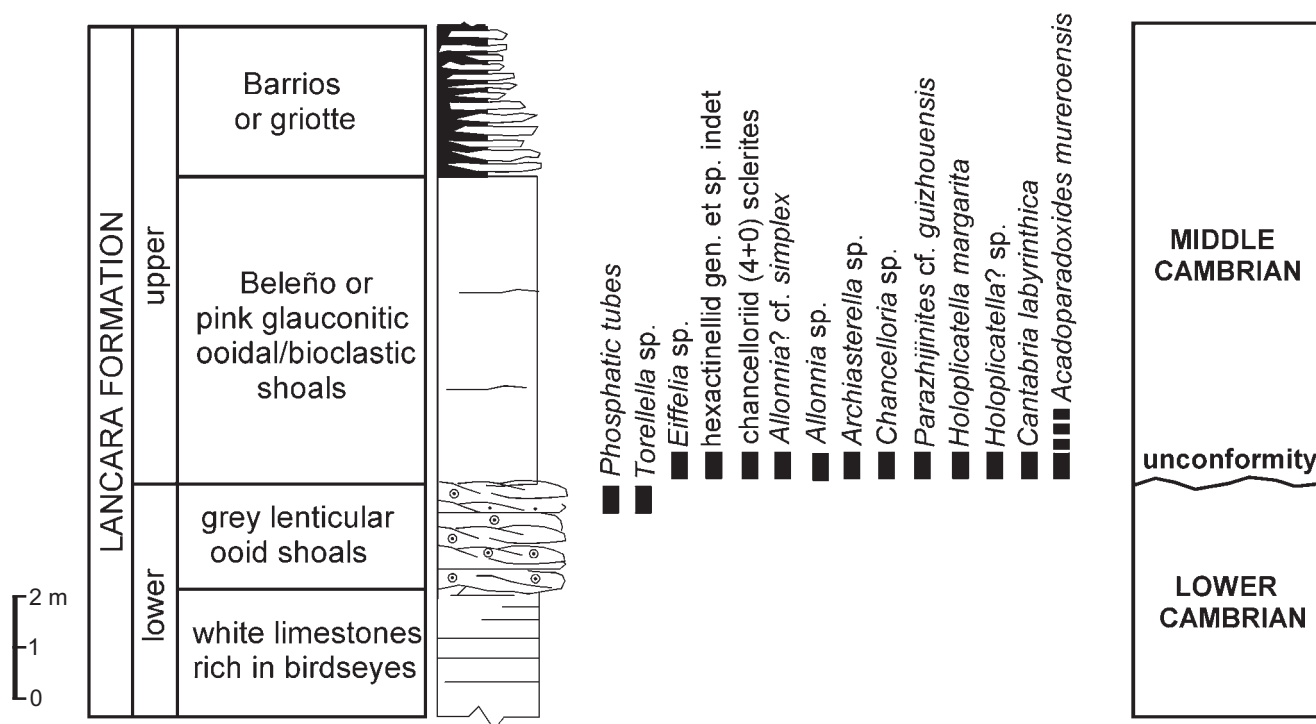


Fig. 2. Stratigraphic units of the Lower–Middle Cambrian boundary interval in the Esla nappe, and setting of the fossils described in the text.

Cambrian boundary. Samples were taken within the uppermost Lower Cambrian ooid-bioclastic limestone, and from the lowermost Middle Cambrian “Beleño” facies of the Lánacara Formation in the vicinity of Valdoré and Crémenes (V_1 and Cr_{1-4} sections, respectively; Fig. 1). Thirty kilograms of limestone were etched with 10% acetic acid. Chemical composition of extracted microfossils was determined using SEM-EDS analyser. Although some of the extracted microfossils were originally phosphatic in composition, the phosphate is commonly the result of diagenetic replacement of the whole skeletons, superficial impregnation, or steinkerns (best preservation is observed in section Cr_4). In the Lower Cambrian samples, released internal moulds were dolomitic with some clay inclusions. Thin sections and backscattered SEM observations help in some cases to recognize the original, unaffected shell microstructure and composition.

Systematic palaeontology

Phylum Porifera Grant, 1836

Class Heteractinida de Laubenfels, 1955

Order Octactinellida Hinde, 1887

Family Eiffeliidae Rigby, 1986

Genus *Eiffelia* Walcott, 1920

Type species: Eiffelia globosa Walcott, 1920; Burgess Shale (Middle Cambrian), British Columbia, Canada.

Eiffelia sp.

Fig. 3A.

Material.—Ten specimens preserved as secondarily phosphatized spicules in the Middle Cambrian “Beleño” facies, sections Cr_2 and Cr_4 .

Description.—The spicules have a regular six-rayed disk, 310–330 μm in diameter, with rays diverging at ca. 60° ; the rays are slender and can be of unequal length (80–200 μm); they usually intersect at a slight angle to the plane of the central disk so that both concave and convex sides are distinguishable; lack of central transverse ray.

Remarks.—Specimens with regular six-rayed basal disk and without transverse central ray show the unquestionably distinctive feature of *Eiffelia*, but both *E. globosa* and *E. araniiformis* share this type of spicule. Even if Bengtson (in Bengtson et al. 1990: 29), considering that species of *Actinoites* Duan, 1984, *Lenastella* Missarzhevsky in Missarzhevsky and Mambetov, 1981, and *Niphadus* Duan, 1984 are synonyms of *E. araniiformis*, noted that “although Middle Cambrian spicules of *E. globosa* with central rays are not known [according to Rigby 1986] the majority of Lower Cambrian spicules similarly lack a central ray. It seems probable that Middle and Lower Cambrian forms had similarly constructed spicular skeletons”, the available material does not include specimens with transverse central ray and therefore *E. araniiformis* cannot be properly identified (Stefan Bengtson, personal communication 2004). However, the few available specimens and their preservation make assignment to *E. globosa* unwarranted. In conclusion, the spicules described above are referred to *Eiffelia* under open species nomenclature.

The specimens reported herein are broadly similar to specimens released from Iberian Chains (Álvarez and Vennin

1996), and to some specimens figured and described by Mehl (1998: 1172) and Bengtson (in Bengtson et al. 1990: fig. 12G).

Class Hexactinellida Schmidt, 1870

Order and family uncertain

Fig. 3B–D.

Material.—More than 100 specimens preserved as secondary phosphatized spicules or phosphatic steinkerns in the Middle Cambrian “Beleño” facies, sections Cr₁ to Cr₄.

Description.—Siliceous hexactine spicules, exhibiting regular triaxons with six rays at right angles displaying the original spicule symmetry of hexactinellids; size variable, from about 0.2 to 0.8 mm in diameter; rays long and inflated with rounded ends; basal diameter of the ray 80–100 μm; in some specimens, the rays radiate from an inflated spherical center reaching 350–400 μm in diameter (Fig. 3D). Normally, the rays are of approximately equal length, but in some specimens a few rays are reduced (probably because of erosion) and, in others, one or two rays reach almost double length. When broken, most of the rays show central canals, and hollow spherical center (Fig. 3D).

Remarks.—Similar inflated hexactines (with inflated rays) have been reported from the Middle Cambrian of Australia (Mehl 1998), and the Upper Cambrian of Argentina (Heredia et al. 1987).

Phylum and Class uncertain

Order Coeloscleritophora? Bengtson and

Missarzhevsky, 1981

Family Chancelloriidae Walcott, 1920

Remarks.—The nomenclature and taxonomy adopted below follow Qian and Bengtson (1989) and Bengtson (in Bengtson et al. 1990) who revised and updated the chancelloriid genera.

Chancelloriid (4+0) sclerites

Fig. 3E–G.

Material.—About 20 specimens preserved as phosphatic steinkerns from the “Beleño” facies, sections Cr₁ to Cr₄.

Description.—Sclerites having four rays (up to 300 μm long, most distal parts eroded off) merging with distinct external boundaries; some sclerites show rays with varying degrees of

curvature (Fig. 3F), others (Fig. 3G) have subrectangular outlines of the foramina-bearing base.

Remarks.—(4+0) sclerites could be assigned to *Allonia* (*A.?* *tetrathallis* sensu Qian and Bengtson, 1989), *Chancelloria* (*C. eros* Walcott, 1920), and *Archiasterella* (*A. cf. hirundo* sensu Bengtson, in Bengtson et al. 1990; *A. pentactina* Sdzuy, 1969). Therefore, and because of the differences in ray curvature observed and the general preservation of the sclerites, the use of open nomenclature seems more appropriate here.

Genus *Allonnia* Doré and Reid, 1965

Type species: *Allonnia tripodophora* Doré and Reid, 1965; Lower Cambrian, Carteret, Armorican Massif, France.

Remarks.—Qian and Bengtson (1989: 19) broadened the concept of the genus [originally including only sclerites with a (3+0) formula] to include sclerites with (2+0) and (4+0) formulas with the rays bending sharply away from the plane of the basal facet.

Allonia? cf. *simplex* (Jiang in Luo et al. 1982)

Fig. 3H, I.

Material.—Ten specimens preserved as phosphatized steinkerns in the Middle Cambrian “Beleño” facies, section Cr₄.

Description.—Two-rayed sclerites (up to 500 μm long, distal part of the rays most probably eroded off) diverging at about a right angle with distinct boundary between the rays.

Remarks.—These specimens are not interpreted as fragments of three- or four-rayed forms because the two rays diverge at a right angle, are straight and lie on the same plane. Although *A. pentactina* (Sdzuy, 1969) has a small percentage of 2+0 sclerites, the present sclerites seem to represent *Allonnia?* cf. *simplex* (Jiang in Luo et al. 1982). However, the foramina are indiscernible because of inadequate preservation of the phosphatic steinkerns

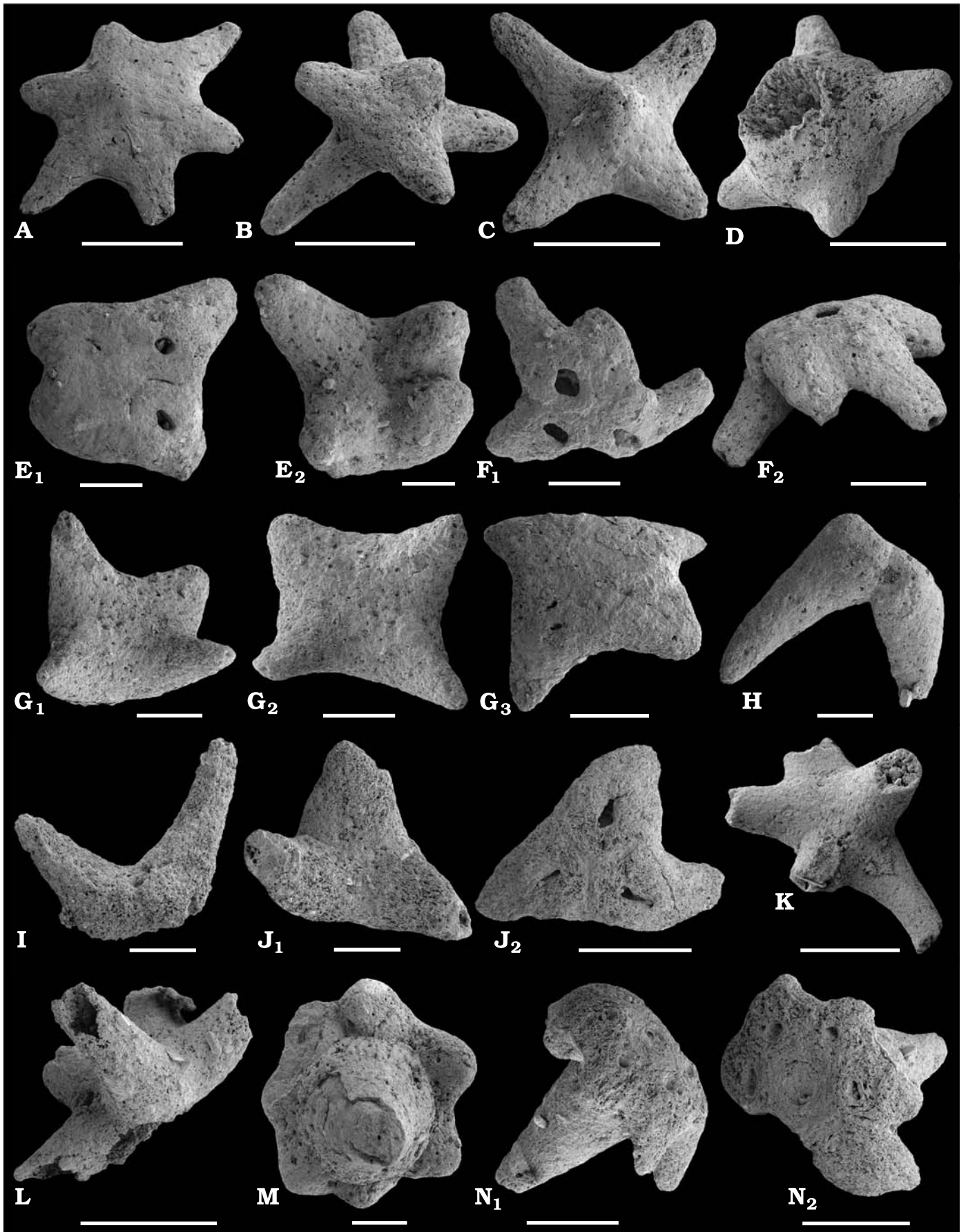
Allonnia sp.

Fig. 3J.

Material.—About 20 specimens preserved as phosphatic steinkerns in the Middle Cambrian “Beleño” facies, section Cr₄.

Description.—(3+0) sclerites (rarely exceeding 0.7 mm of length, most distal parts of the rays eroded off) having rays of equal width, thin, slender, and tapering, each with a round to weakly elliptical aperture (foramen) located on a swollen base.

Fig. 3. Scanning electron micrographs of skeletonized microfossils from the lowermost Middle Cambrian of the Esla Nappe, Cantabrian Mountains, Spain. →
A. *Eiffelia* sp.; heteractinid sponge spicule, section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian; DGO 21116. **B–D.** Hexactinellid sponge spicules; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian; DGO 21117–21119. **E–G.** Chancelloriid (4+0) sclerites; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **E.** DGO 21120, basal (E₁) and upper (E₂) views. **F.** DGO 21121, basal (F₁), and lateral (F₂) views. **G.** DGO 21122, upper (G₁, G₂) and basal views (G₃). **H, I.** *Allonnia?* cf. *simplex*; chancelloriid sclerites, section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian; upper views, DGO 21123–21124. **J.** *Allonnia* sp.; chancelloriid sclerite, section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian; DGO 21125. **K, L.** *Archiasterella* sp.; incomplete chancelloriid sclerites; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **K.** DGO 21126, upper view. **L.** DGO 21127, oblique view. **M, N.** *Chancelloria* sp. A; chancelloriid sclerites; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **M.** DGO 21128, upper view. **N.** DGO 21129, lateral (N₁) and basal (N₂) views. Scale bars 250 μm.



Remarks.— Even if there is good evidence from completely preserved Burgess Shale cancelloriids that at least some forms with *Allonia tripodophora*-type sclerites (*C. eros* Walcott, 1920 type 2 *sensu* Bengtson, in Bengtson et al. 1990) have a unimembrate scleritome with three rays in each spicule, variability within the *Allonia* scleritome remains poorly known (see for example *A. junyuani* Janussen et al. 2002). *Allonia tripodophora* differs from *A. erromenosa* Jiang in Luo et al. 1982, also (3+0), in the presence of a distinct external boundary between the rays and an angle of approximately 45–80° from the basal plane. *C. racemifundis* Bengtson, 1990 (in Bengtson et al. 1990), which may also contain 3-rayed sclerites, differs in the shape of the base. Formal comparisons with the various *Allonia* species are precluded because of the inadequate, phosphatic-steinkern preservation of the cancelloriid sclerites described here. In conclusion, open nomenclature seems more appropriate for these specimens.

Genus *Archiasterella* Sdzuy, 1969

Type species: *Archiasterella pentactina* Sdzuy, 1969; Lower Cambrian (Atdabanian), Cazalla de la Sierra, Ossa Morena, Spain.

Archiasterella sp.

Fig. 3K, L.

Material.—Twelve specimens preserved as phosphatized sclerites or phosphatic steinkerns in the Middle Cambrian “Beleño” facies, section Cr₄.

Description.—5+0 sclerites having one median recurved ray (up to 200 µm long), and four lateral rays (up to 300 µm long), all incompletely preserved.

Remarks.—Among *Archiasterella* species, 5+0 sclerites occur in *A. pentactina* Sdzuy, 1969 (with 2+0 and 5+0 sclerites), *A. antiqua* Sdzuy, 1969 (with 2+0 and 4–7+0 sclerites), and *A. robusta* Vasilieva, 1986 (with 5+0 sclerites). The latter, which differs only from *A. pentactina* in the robust character of its axis, may be considered as a junior synonym of this species. The incomplete preservation of the Cantabrian sclerite rays prevents a definite assignment to any species.

Genus *Chancelloria* Walcott, 1920

Type species: *Chancelloria eros* Walcott, 1920; Burgess Shale, Middle Cambrian, British Columbia, Canada.

Chancelloria sp. A

Figs. 3M, N, 4A, B.

Material.—About 20 specimens from the Middle Cambrian “Beleño” facies, section Cr₄.

Description.—Sclerites with a tapering central vertical ray (0.5 to 0.7 mm in length) and five to seven prominent, recurved, radiating lateral rays; lateral rays are asymmetrically arranged and commonly differ in size; the curvature of rays is greatest at the intersection with the central ray; they are relatively straight, and make an acute angle (less than 30°) with the central ray; diameter of the sclerite can reach 0.6 mm, whereas the maximum diameter of the central ray is 0.4 mm; specimens commonly have five to six lateral rays, although a

few have seven; they are oval to subrectangular in cross-section, except for the tips, which are round in outline, whereas the whole central ray is round in cross-section except at its polygonal base; specimens are slightly longer (central ray) than large (including lateral-ray outline), with a ratio varying from 1 to 1.5. Specimens cut longitudinally (Fig. 4A) show an inner cavity along the central ray, subtriangular in section, bounded (except at the basal foramen) by a wall, ca. 30 µm thick.

Remarks.—Some specimens of *Chancelloria eros* from the Lower Cambrian of the United States (Mehl 1996: fig. 1D) and the Middle Cambrian of Australia (Mehl 1998: pl. 7: 7–8) show similar robust rays, although they have a distinct flat base and flat marginal rays, and the Cantabrian sclerites are prominently recurved. The morphology of the Cantabrian sclerites mimics that of paraclavules, interpreted as anchorate root-tuft spicules by Mehl (1996) in hexactinellids associated with dermal or gastral membranes (Mehl 1998), and is also similar to the siliceous spicules of *Nabaviella* Mostler and Mosleh-Yazdi, 1976 (*sensu* Bengtson et al. 1990). Nevertheless, they do not only differ in their composition (most probably secondarily phosphatized calcareous sclerites, not siliceous in origin) but also in the presence of basal foramina. Although some Late Cambrian–earliest Ordovician pelmatozoan holdfasts share close morphological similarities, their size, microstructure and inner cavities are different (Sumrall et al. 1997; Álvaro and Colchen 2002).

Chancelloria sp. B

Fig. 4C–E.

Material.—More than 50 specimens preserved as phosphatic steinkerns in the Middle Cambrian “Beleño” facies, sections Cr₂ to Cr₄.

Description.—Radially symmetrical sclerites with central vertical ray (up to 300 µm long), and 5 to 7 lateral rays lying on the same plane, which can be approximately of equal (ca. 300 µm) or variable (200 to 400 µm) length (though most distal parts of the rays probably eroded off). A broken specimen (Fig. 4E) shows circular transverse sections of rays.

Remarks.—The Cantabrian species is relatively similar to other previously described sclerites, such as those from the Early Cambrian of Southern Spain (Ossa-Morena Zone; Fernández-Remolar 2001: fig. 4a, b) and Antarctica (Wrona 2004: fig. 6j); and from the Middle Cambrian of Australia (Mehl 1998: pl. 7: 3); however, the lateral rays of the Cantabrian specimens lie on the same plane whereas they are clearly bent in the others. The sclerites referred to as *Chancelloria* sp. A above differ from *Chancelloria* sp. B. in the significantly larger central ray and prominently recurved lateral rays.

Phylum uncertain

Class Cambroclavida Conway Morris and Chen, 1991

Family Zhijinitidae Qian, 1978

Genus *Parazhijinites* Qian and Yin, 1984

Type species: *Parazhijinites guizhouensis* Qian and Yin, 1984; Meishucunian (Lower Cambrian), Guizhou, China.

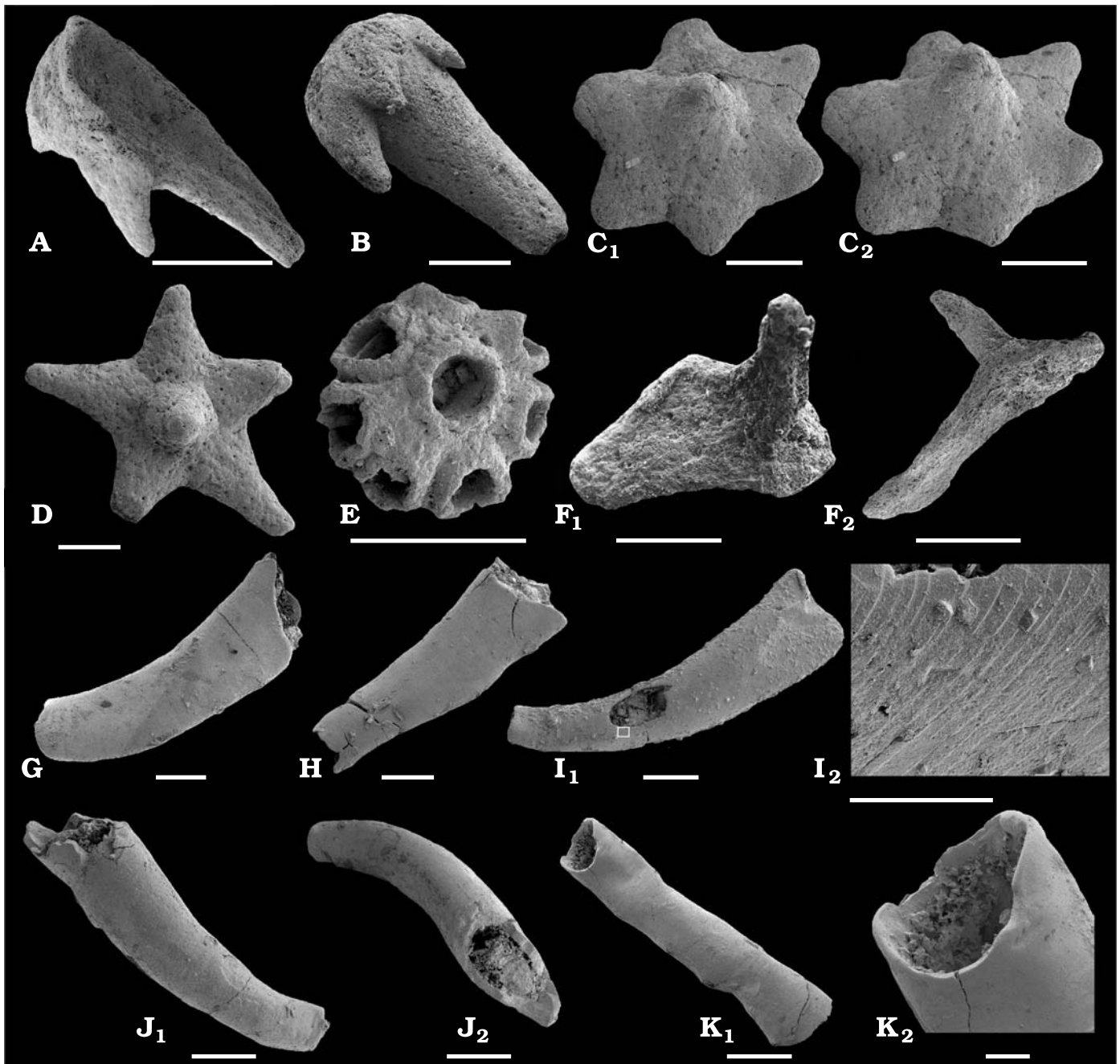


Fig. 4. Scanning electron micrographs of skeletonized microfossils from the Lower–Middle Cambrian transition of the Esla Nappe, Cantabrian Mountains, Spain. **A, B.** *Chancelloria* sp. A; chancelloriid sclerites; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **A.** DGO 21129, longitudinal section. **B.** DGO 21130, lateral view. **C–E.** *Chancelloria* sp. B; chancelloriid sclerites; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **C.** (1+6) sclerite, DGO 21131, lateral views. **D.** (1+5) sclerite, DGO 21132, upper view. **E.** Incomplete (1+7) sclerite, DGO 21133, upper view. **F.** *Parazhijnites* cf. *guizhouensis* Qian and Yin, 1984; cambroclavid sclerite; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian; DGO 21134, oblique (F₁) and lateral (F₂) views. **G–J.** *Torellella* sp.; hyolithelminth tubes; section Cr₄, ooid/bioclasic limestone, lower member of the Láncara Formation, latest Early Cambrian. **G.** DGO 21135, lateral view. **H.** 21136, lateral view. **I.** DGO 21137, lateral view showing elliptic perforation (I₁) and detail of the faint growth lines (squared area on I₁; tilt adjust). **J.** DGO 21138, lateral (J₁) and distal (J₂) views. **K.** Phosphatic undefined tube; section Cr₄, ooid/bioclasic limestone, lower member of the Láncara Formation, latest Early Cambrian; DGO 21139, lateral view (K₁) and detail of broken termination (K₂). Scale bars 250 μm, except I₂ and K₂ for which are 50 μm.

Parazhijnites cf. *guizhouensis* Qian and Yin, 1984

Fig. 4F.

Material.—Two phosphatic sclerites from the Middle Cambrian “Beleño” facies, section Cr₄.

Description.—Elongate sclerites, subhexagonal in outline and posteriorly expanded (650 μm long and 400 μm wide), bilaterally symmetrical; anterior spine perpendicular to slightly bent at its extremity (400 μm long), with oval cross-section

(160 μm in diameter), except at its tip where it is round; surface smooth.

Remarks.—Bengtson et al. (1990) indicated that cambroclavids exhibit a wide morphological variability within the same scleritome, so that additional material seems necessary to complete the description and systematic assignment of the Cantabrian taxon. *Parazhijinites guizhouensis* shows a widespread morphological variability, and the most noticeable feature of this species is the elongate spine arising from a small base (Conway-Morris et al. 1997: 179). Although Conway Morris and Chen (1991) placed questionably *Z. guizhouensis* Qian and Yin, 1984 in synonymy with *Z. longistriatus* Qian, 1978, the former only differentiable by the presence of a slipper-like base and a very elongate spine, Conway Morris et al. (1997) reported them as separate species. The Cantabrian sclerites have all the characters visible in some Chinese sclerites of Meishucunian (Zhou et al. 2001: 212, fig. 4.2) to Atdabanian (Conway Morris et al. 1997) age. This paper reports the youngest occurrence of *Parazhijinites* within the lowest trilobite biozone of the Iberian Middle Cambrian.

Phylum and class uncertain

Order Hyolithelminthes Fisher, 1962

Family Torellestidae Holm, 1893

Genus *Torellestia* Holm, 1893

Type species: *Torellestia laevigata* (Linnarsson, 1871), by original designation, Lower Cambrian, Lugná, Västergötland, Sweden.

Torellestia sp.

Fig. 4G–K.

Material.—More than 100 phosphatic tubes and fragments from Lower Cambrian ooid packstones, sections V₁ and Cr_{1–4}.

Description.—Phosphatic, elongated, tube fragments of narrow shape and elliptical cross-section. Keels are faint or not developed. Tubes show a distinct irregular and curved growth pattern, both laterally and dorsoventrally. Thickness of tube-walls ranges between 5 to 15 μm . No different shell-layers are visible. The angle of divergence is not constant and increases sharply near the narrowest (proximal) part of the tube. The largest (distal) part of each tube is clearly more elliptical in cross-section. Most specimens display faint growth lines (furrows; Fig. 4G, H) and/or faint, oblique to transverse riblets (Fig. 3I) on outer surfaces: these structures are sometimes very

regular to relatively irregular, and depend on the relative position of the curvature. Ring-like or other morphological characters are not observed on outer surfaces.

Remarks.—Even if the multi-layered structure of the wall is rarely preserved, external morphological characters of these tubes can be related to *Torellestia lentiformis* (Sysoyev, 1960). However, Sysoyev (1962) described the lateral keels in this species as “sharp”, and Sokolov and Zhuravleva (1983) as “distinct”, in contrast with the “faint or not developed” keels of the Cantabrian sclerites. Calcitic skeletons, described in thin section, including hyolith, trilobite and echinoderm remains (Álvaro et al. 2000b), were not released from limestones owing to lack of epigenesis; as a result, it can be assumed that the composition of etched specimens was phosphatic in origin. Numerous specimens exhibit rounded to elliptical holes on their walls (Fig. 4I). Even if their shape and the original phosphatic composition of the walls suggest they are active perforations (bioerosion and/or predation), they may be related to preservational artifacts, and thus, further study is needed before to conclude on their formation pattern.

Numerous unidentified phosphatic (fragmented) tubes occur with *Torellestia* sp. One of these phosphatic tubes (Fig. 4K), 0.8 mm long, is broadly straight, with a circular to irregularly deformed cross-section (up to 150 μm in diameter), curved irregularities and exhibits an angle of divergence of its subparallel sides of ca. 5°. The circular cross-section suggests relationship either with *Hyolithellus* or other tubular taxa (either phosphatic or calcareous in origin). Nevertheless, the buckled appearance, which is difficult to differentiate from deformational features, is unusual in this genus. In conclusion, this tube cannot be properly assigned within the hyolithelminths.

Phylum uncertain

Class Hyolitha Marek, 1963

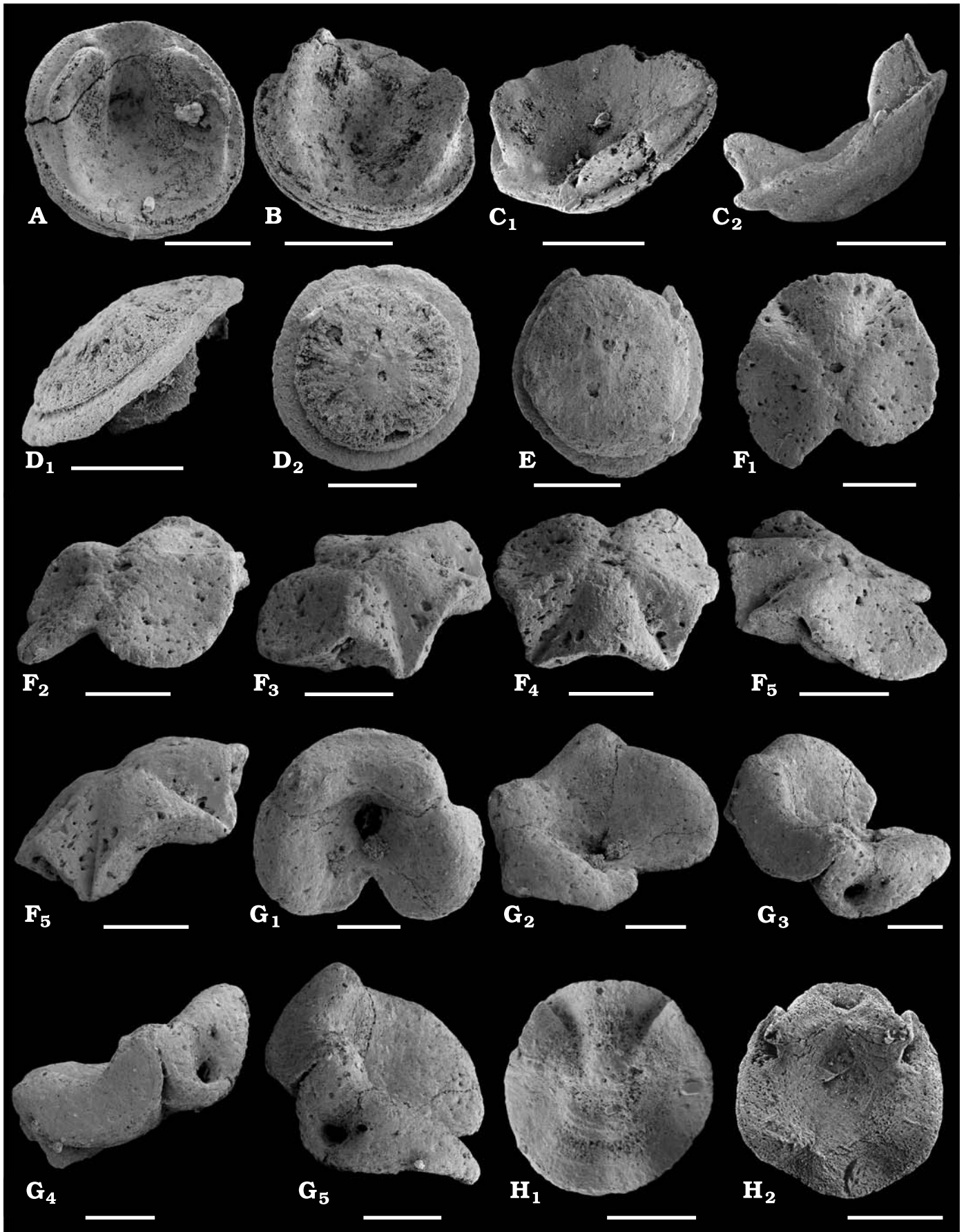
Subclass Orthothecimorpha Sysoyev, 1968

Remarks.—Qian and Xiao (1995) have recently proposed a relatively comprehensive hyolith classification (see English translation in Kruse 2002). Due to the lack of conchs associated with opercula, detailed suprageneric-level groupings will not be used herein.

Operculum A

Fig. 5A–E.

Fig. 5. Scanning electron micrographs of skeletonized microfossils from the lowermost Middle Cambrian of the Esla Nappe, Cantabrian Mountains, Spain. →
A–E. Operculum A, orthothecimorph hyolith; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **A.** DGO 21140, internal view. **B.** DGO 21141, oblique internal view of margin. **C.** DGO 21142, oblique internal view of margin (C₁) and lateral view (external side oriented downward; C₂) showing correspondence between outer peripheral margin and internal marginal zone. **D.** DGO 21143, lateral view (external side oriented upward; D₁) and external view (D₂) showing distinct peripheral band. **E.** DGO 21144, external view showing faint concentric growth lines within central area. **F, G.** *Holoplicatella margarita* gen. et sp. nov.; enigmatic fossil, part of a larger scleritome or operculum in function; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian. **F.** DGO 21145; convex face (F₁, posterior margin oriented downward); oblique, postero-lateral view (F₂); oblique posterolateral view (F₃); oblique anterolateral view (F₄); lateral view (F₅); anterior view (F₆). **G.** DGO 21146, holotype; concave face (G₁; posterior margin oriented downward); oblique posterolateral view (G₂); oblique anterolateral view (G₃); anterolateral view (G₄); and lateral view (G₅). **H.** *Holoplicatella?* sp.; enigmatic fossil, part of a larger scleritome or operculum in function; section Cr₄, “Beleño” facies, upper member of the Láncara Formation, early Leonian; DGO 21147, concave (H₁) and convex (H₂) faces (anterior margin oriented upward). Scale bars 250 μm .



Material.—About 20 phosphatized opercula from the “Beleño” facies, section Cr₄.

Description.—Operculum circular to slightly oval in outline, up to 0.6 mm in diameter; outer side strongly convex and smooth, with faint concentric growth lines, composed of a central, convex (sometimes almost hemispherical) area separated by a distinct depression from a peripheral band, corresponding to internal marginal zone and reaching ca. 1/10 of the diameter; well rounded apex (growth center) situated generally in the centre of the operculum or slightly excentric; inner (concave) side bearing a distinctly offset marginal zone, up to about 1/10 of the operculum diameter in width; paired cardinal processes prominent, crescent-shaped, symmetrically bounding internally the offset marginal zone, diverging at 30–40° at their most prominent edge, and reaching 4/5 of the diameter; clavicles absent.

Remarks.—The Cantabrian operculum differs from *Conotheca australiensis* Bengtson (in Bengtson et al. 1990) and *C. laurentiensis* Landing and Bartowski, 1996 (respectively from the Lower Cambrian of Australia and Laurentia), in the absence of clavicle-like tubules. It differs also from *Turcutheca?* sp. A (Hinz 1987), from the Lower Cambrian of Shropshire (UK), in the crescent shape of the cardinal processes; from *Sysoieva exilis* Marek, Malinky and Geyer, 1997, from the Middle Cambrian *Micmacca* Breccia, in the shape of the cardinal processes (like wings of butterfly) and central termination of their lateral edges, attached to the interior surface and terminating in a central point; and from *Neogloborilus hymenodes* (Duan and Xiao in Qian et al. 2000), from the Lower Cambrian Yuertus Formation, Xinjiang (China), in the presence of a central elevated area (ca. 1/3 of the diameter) lacking a central apex on the convex side, and of paired cardinal processes bearing transverse faint constrictions on the concave side. As Marek (1963) pointed out that hyolith taxa should not be erected without complete information from both conch and operculum morphology, the present operculum is taxonomically unassigned.

Phylum, class, order and family uncertain

Genus *Holoplicatella* nov.

Etymology. From *Triplicatella* Conway Morris (in Bengtson et al. 1990), a Lower Cambrian sclerite remarkably similar to the new genus erected here, and *holos* (greek), complete. *Holoplicatella* (feminine): sclerites with characteristic plication of their entire surface.

Type species: *Holoplicatella margarita* gen. et sp. nov.

Diagnosis.—As for the species (because of monotypy).

Remarks.—Although *Triplicatella* was interpreted as the earliest polyplacophoran (Yates et al. 1992), their shape and putative muscle scars, and their occurrence as internal molds sealing the aperture of a hyolith-like conch (Demidenko in Gravestock et al. 2001) are suggestive of an operculum function (Bengtson et al. 1990; Conway Morris and Peel 1995). Skovsted (2003) has recently proposed to place *Triplicatella* in a still undefined “hyolith stem group”. *Holoplicatella* gen. nov. might be interpreted as a part of a larger scleritome of

uncertain affinity, although an operculum function cannot be rejected.

Holoplicatella margarita gen. et sp. nov.

Fig. 5F, G.

Etymology. After “margarita” (in Spanish, daisy), the broad aspect of the convex side of the sclerite.

Type locality: Eastern Esla nappe, in the vicinity of the locality of Crémenes, Cantabrian Mountains, Spain.

Type horizon: Up to 10 m above the base of the “Beleño” facies, upper member of the Lánacara Formation.

Holotype: Sclerite DGO 21146 (Fig. 5G).

Material.—Eight specimens from the “Beleño” facies, section Cr₄.

Diagnosis.—Bilaterally symmetrical, concavo-convex sclerites, oval to subtrapezoidal in outline, bearing one prominent notch and two subduded domes on concave side, two distinct pits and radially symmetric folds or invaginations on anterolateral margins.

Description.—Two faces, convex and concave, can be distinguished in these sclerites. One margin of the sclerite bears a prominent notch, and is here considered (by analogy with marginal notches of *Wushichites*; Conway Morris et al. 1997) as the posterior margin. On the convex face, the opposite (anterior) margin bears two symmetrical (perpendicular) folds or invaginations, which form prominent sulci on margin, and attenuate toward the centre. The lateral margins connecting both folds and the posterior notch are slightly convex-concave in a rounded sinuous pattern that also attenuates toward the centre. The anterior margin of the concave face bears two symmetrical domes with rounded tops, which correspond to the prolongation of the above-described folds, connected by a faint depression, the whole framework elevated above the rest of the face; the centre of the concave face is depressed anteriorly and laterally bounded by an amphitheatre-like wall. The lateral (concave upward) view of the sclerite is subtriangular, increasing in thickness toward the anterior margin, and bears two lateral pits (60 µm in outer diameter) in the wall at both anterolateral sides.

Comparison.—*Wushichites minutus* and *W. polyedrus* were originally defined in Xinjiang (China) by Qian and Xiao (1984) as cambroclaves of uncertain affinity. Although Bengtson et al. (1990: 103) reported both taxa as “doubtful species” likely referable to the genus *Cambroclavus*, their morphological characters are so striking that it seems reasonable to place them in a separate genus (Conway Morris et al. 1997). These authors revised new material from the type area, and considered *W. polyedrus* to be a junior synonym of *W. minutus*. The presence of a prominent spine broadly transverse to the disc (Qian Yi 1989: 235) was the criterion for keeping *Isoclavus* and *Wushichites* separate (Conway Morris et al. 1997: 180). *Holoplicatella* differs from *Wushichites* sensu Conway Morris et al. (1997) in the presence of folds and lateral pits, and the broadly inflated (and not flattened) character of the sclerites.

Triplacatella (Bengtson et al. 1990; Skovsted 2003) is composed of bilaterally symmetric, concavoconvex sclerites, with strongly developed folds and invaginations concentrated at both margins of the axis of symmetry. In contrast, *Holoplicatella* has a prominent notch (as in *Wushichites*) and two anterolateral pits.

Stratigraphic and geographic range.—Lowermost Middle Cambrian “Beleño” facies, upper member of the Láncara Formation, eastern Esla nappe, in the vicinity of the locality of Crémenes, Cantabrian Mountains, Spain.

Holoplicatella? sp.

Fig. 5H.

Material.—One isolated specimen from the “Beleño” facies, section Cr₄.

Description.—Bilaterally symmetric, concavoconvex sclerite, ca. 750 µm in diameter. The convex face of the sclerite is subcircular in outline, bearing two pairs of distinct symmetric folds on the anterolateral half of the face. The anterior margin of the concave side bears two lateral symmetric, sharp-pointed domes, which correspond to the prolongation of the above-described folds, connected by an offset marginal platform, U-shaped, and bounded by steep slopes. In lateral view, both domes and the platform are prolonged into a subtriangular face bearing a central pit, circular in outline and 120 µm in diameter. The posterior margin of the concave face is depressed, connected with the center of the concavity and with the steep slopes that bound the U-shaped offset marginal platform. The posterior margin is rounded and has no notch.

Remarks.—Although the specimen is morphologically close to *Holoplicatella margarita* gen. et sp. nov., open nomenclature is preferred: *Holoplicatella?* sp. differs from *P. margarita* in the absence of a prominent notch on the posterior margin, and the presence of two pointed domes on the anterior margin and of a distinct pit on the anterior margin of the sclerite. These characters do not seem preservational artifacts and are maintained here as morphologically distinctive.

Genus *Cantabria* nov.

Type species: *Cantabria labyrinthica* gen. et sp. nov.

Etymology: After the Cantabrian Mountains, in which the fauna was sampled. *Cantabria* (feminine): enigmatic sclerite from the Cantabrian Mountains.

Diagnosis.—As for the species (because of monotypy).

Cantabria labyrinthica sp. nov.

Figs. 6–8.

Etymology: After “labyrinthine”, the diagnostic character of the meshwork microstructure.

Type locality: Eastern Esla nappe, in the vicinity of the locality of Crémenes, Cantabrian Mountains, Spain.

Type horizon: Up to 10 m above the base of the “Beleño” facies, upper member of the Láncara Formation.

Holotype: Plate DGO 21149 (Fig. 6B).

Material.—More than 100 specimens preserved as phosphatic sclerites in the “Beleño” facies, sections Cr₂ and Cr₄.

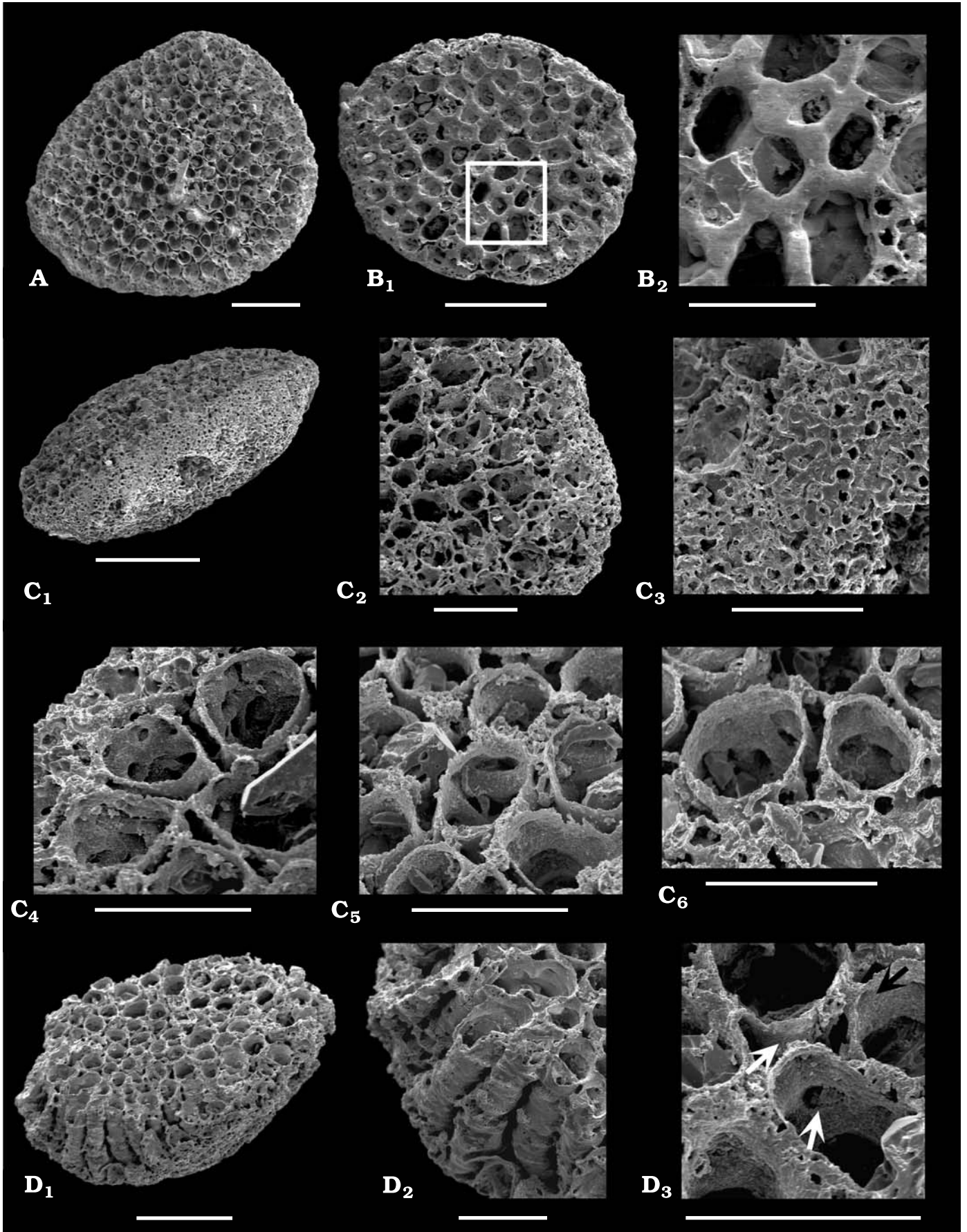
Diagnosis.—Phosphatic sclerites, subcircular in outline and trapezoidal in cross-section, composed of a labyrinthine meshwork of tubes that centripetally increase in diameter and length; tubes interconnected by transverse smaller tubes; upper surface perforated by meshwork of holes, round to oval in shape.

Description.—Phosphatic sclerites, subcircular in outline and trapezoidal in cross-section, with flat bottom, up to 0.8 mm in diameter and 0.2 mm thick, constructed of two parts: a framework forming a labyrinthine meshwork of tubes, and an upper surface making up the uppermost wall junctions of tubes; in some cases the latter is absent because of erosion or incomplete preservation. Edge of sclerites formed by peripheral girdle, completely perforated: holes 5–15 µm in diameter on bottom and lateral sides, and 50–200 µm on upper cap. Basal and lateral girdle rough containing grooves joining small perforations. Upper surface usually flat to slightly convex, perforated by meshwork of holes, round to oval in shape, highly variable in size (from 50 to 200 µm in diameter) but distinctly decreasing in size close to periphery; wall junctions between holes thin (ca. 30–35 µm) and smooth.

Thin sections through sclerites (Fig. 7) reveal a complex internal structure, composed of a labyrinthine meshwork of tubes centripetally increasing in diameter and length by anastomosing their walls (Fig. 8); lowermost and lateral tubes randomly oriented, closed basally by thin hemispherical but perforated part of framework, passing upward into vertical, parallel and larger tubes, with annulated walls (Fig. 7A, B, see also Fig. 6D₁–D₂). Tubes laterally perforated by transverse small synaptical-like tubes, up to 10 µm in diameter, connecting neighboring tubes (Fig. 7E₃, see also Fig. 6D₃). As a result, whole tube meshwork (and, originally, soft parts filling it) intercommunicating. Tube walls composed of two distinct apatitic layers, possibly diagenetic in origin (see discussion below), 0.25–0.3 µm thick (Fig. 7E₂, E₃).

Remarks.—*Cantabria labyrinthica* may be related to the eoconchariids based on the characters observed on the upper surface: the lack of protruding nodes or spines on the wall junctions separating the chaotic hole meshwork is a character shared by *Fusuconcharium* Hao and Shu, 1987. However, the holes of *Microdictyon* Bengtson, Matthews, and Missarzhevsky (in Missarzhevsky and Mambetov 1981), *Fusuconcharium* and *Quadratopora* Hao and Shu, 1987 (even if the two latter are considered synonyms of the former) can be both open and closed basally, are laterally unperforated, and continue as a single assemblage of parallel tubes through the plate, which has a bidimensional shape lacking a cup-shaped form.

The labyrinthine microstructure of *Cantabria* can also be related to stereom microstructures (see e.g., Bengtson et al. 1990: fig. 174A–C; Clausen and Smith 2005). Nevertheless, a labyrinthic stereom (Smith 1980: 12), which would be the most comparable known echinoderm-microstructure, con-



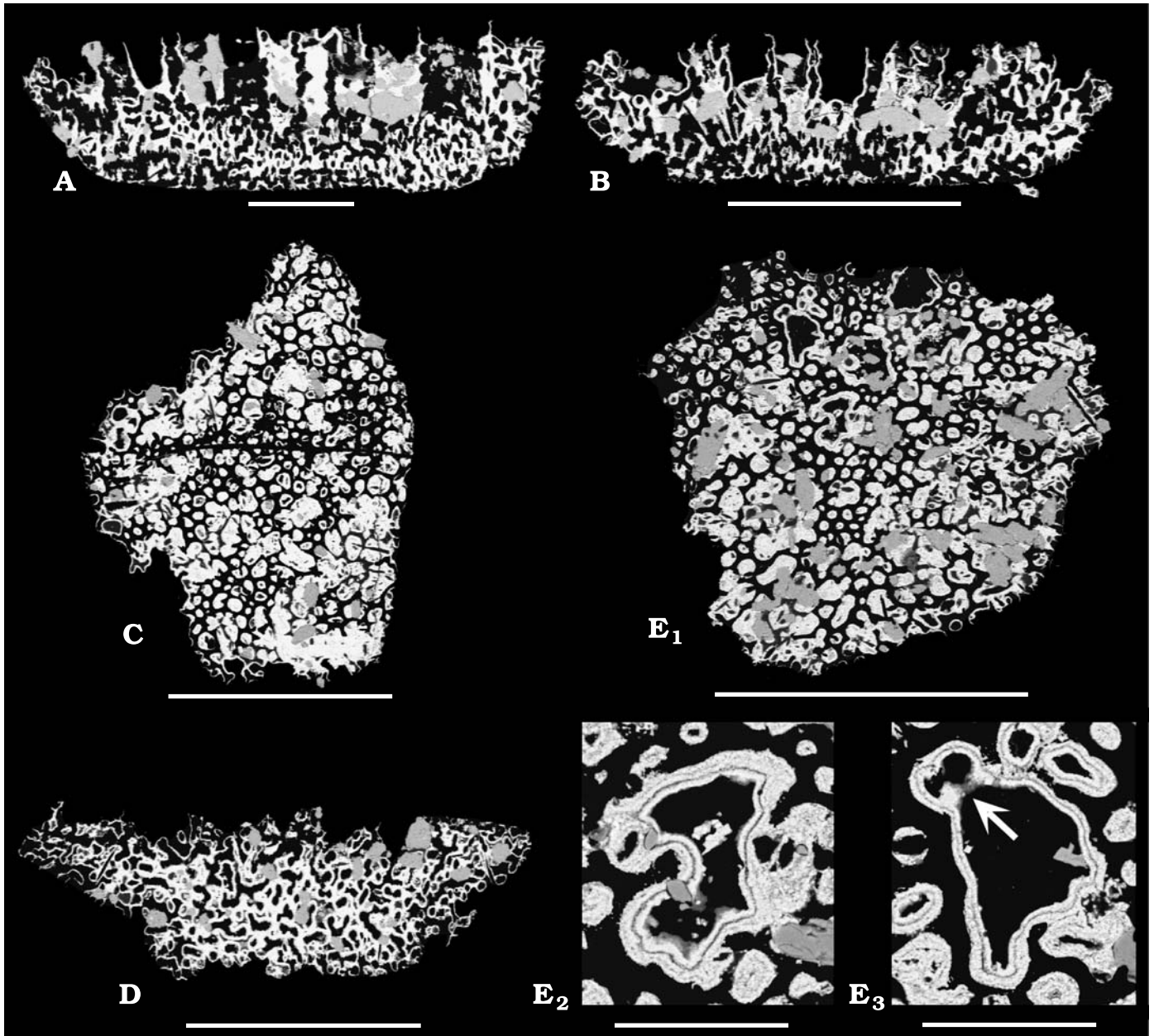


Fig. 7. Thin sections on backscattered SEM of *Cantabria labyrinthica* gen. et sp. nov. (apatite is white and secondary silica is grey), enigmatic fossil, possible external sclerite of lobopodian affinity from the “Beleño” facies (section Cr₄), upper member of the Láncara Formation, early Leonian. **A, B, D.** Cross-sections with chaotic meshwork microstructure of the sclerites (DGO 21152, DGO 21153, and DGO 21156 respectively) with tubes centripetally increasing in size; note their whole perforated pattern of outer wall. **C, E.** Transverse sections close to the basal (**C**, DGO 21154) and the upper side (**E**, DGO 21155) with subcircular to irregular sections of individual tubes. Overall view (**E₁**) and enlargements (**E₂**, **E₃**) showing the tube walls built of two distinct apatitic layers; see a synapticule-like tube (arrowed) connecting two transverse tubes (**E₃**). Scale bars 250 μ m.

← Fig. 6. Scanning electron micrographs of *Cantabria labyrinthica* gen. et sp. nov., enigmatic fossil, possible external sclerite of lobopodian affinity from the “Beleño” facies (section Cr₄), upper member of the Láncara Formation, early Leonian. **A.** DGO 21148; incomplete plate without preserved wall-junctions, but showing the distinct chaotic meshwork. **B.** DGO 21149; holotype, dorsal view of a complete plate (**B₁**), and detail of the smooth wall junctions (**B₂**). **C.** DGO 21150; contact between upper and lateral sides (**C₁–C₃**) showing the change in diameter of perforations, and details of the top of tubes with lateral perforations connecting the framework via synapticules (**C₄–C₆**). **D.** DGO 21151; lateral views of sclerite with annulated tubes (**D₁**, **D₂**) and details of three lateral perforations (arrowed) connecting neighboring tubes in (**D₃**). Scale bars 100 μ m, except A, **B₁**, **C₁**, and **D₁** for which are 250 μ m.

sists of an unorganized mesh of trabeculae (which are not hollow) that behaves as a single crystal, whereas the meshwork of *Cantabria* is composed of (hollow) tubes with walls containing two distinct apatitic layers (Fig. 7E₂, E₃), al-

though this last character may be diagenetic. These skeletons were either originally phosphatic in composition or secondarily replaced by phosphate. However, the apatitic meshwork is not likely to represent phosphatic crusts lining trabe-

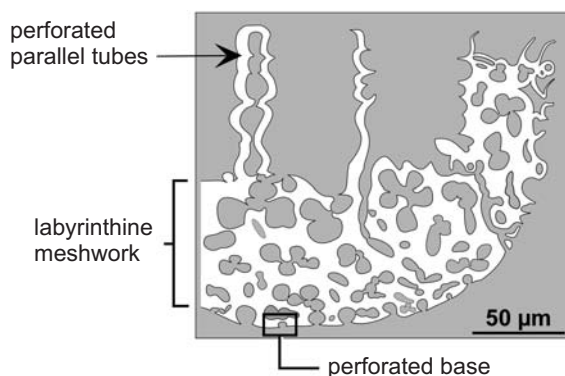


Fig. 8. Sketch of *Cantabria labyrinthica* gen. et sp. nov. (enigmatic fossil, possible external sclerite of lobopodian affinity) illustrating the cross sections of the previous figure.

culae and pores (external molds) as they have a constant wall thickness and both their inner and outer sides are ornamented with transverse crests (Fig. 6C). In addition, although the “Beleño” facies is dominated by “encrinitic” (echinoderm-rich) packstone (see Álvaro et al. 2000b), echinoderm ossicles are absent after etching as they were not secondarily phosphatized: phosphatization was selective and did not apparently affect stereoms. In summary, even if we interpret the described structure as a coated stereom, the preservation of the upper surface of the plates (Fig. 6B, D) indicates that their tubes would form a stereom porosity and, therefore, the density, coarseness (*sensu* Smith, 1980) and structure would be quite different from other known stereom types.

The taxonomic affinity of *Cantabria* is uncertain. Nevertheless, the similarities with eoconchariids (discussed above) suggest it might be considered as Middle Cambrian lobopodian external sclerites phylogenetically related to the Early Cambrian eoconchariids. However, new sclerites found in other outcrops, and eventually with other mineralogical composition, would help to improve this uncertain assignment.

Stratigraphic and geographic range.—Lowermost Middle Cambrian “Beleño” facies, upper member of the Láncara Formation, eastern Esla nappe, in the vicinity of the locality of Crémenes, Cantabrian Mountains, Spain.

Discussion: benthic community replacements

The regional unconformity located at the top of the ooid-bioclasic shoals that crop out in the Esla nappe is the boundary between the lower and upper members of the Láncara Formation and the Iberian Lower–Middle Cambrian boundary. The uppermost Lower Cambrian sedimentary rocks represent a ramp with ooid-bioclasic shoals that favored the development of protected archaeocyathan-microbial reefs (see taphonomic, sedimentologic, and sequence-stratigraphic analyses in Álvaro et al. 2000b). The shoals have yielded abundant debris of tubular shelly fossils, such as hyoliths

(abundant in thin section but not phosphatized, so badly preserved after etching) and hyolithelminths (*Torellia*), and trilobites. Above the erosive unconformity, a different benthic community occurs in the overlying glauconitic limestone, and is associated with development of widespread low-relief bioclasic shoals. Their lowermost part is rich in hexactinellid and heteractinid sponge spicules (*Eiffelia*), cancelloriid sclerites (*Allonnia*, *Archiasterella*, and *Chancelloria*), and cambroclaves (*Parazhijinites*), possible eoconchariids (*Cantabria* gen. nov.), other sclerites of uncertain affinity (*Holoplicatella* gen. nov.), echinoderm ossicles, calcite-shelled brachiopods, and trilobites. Although both bioclasic shoals represent similar high-energy conditions (Álvarez et al. 2000b), the Iberian Lower–Middle Cambrian boundary marks a drastic change in microfossil assemblage. Obviously, this observation is taphonomically biased: only originally phosphatic tubes and dolomitized steinkerns have been released from the Lower Cambrian level whereas phosphatic and secondarily phosphatized microfossils and internal moulds were analyzed after etching from Middle Cambrian limestones. Nevertheless, the secondary phosphatization described in the Middle Cambrian samples was also selective, as it did not affect echinoderm remains. Moreover, even originally siliceous spicules (e.g., hexactinellids) or phosphatic sclerites give relevant clues of change in biodiversity. This can be related to a community replacement from hyolithelminth-phosphatic tubular to CES (cancelloriid-echinoderm-sponge) meadows (echinoderm ossicles, although seemingly unaffected by phosphate replacement, are extremely abundant in thin section), dominated by filter/suspension feeders (spiculate sponges, cancelloriids, calcite-shelled brachiopods, echinoderms, hyoliths and hyolithomorphs), in which eoconchariids? and trilobites illustrate sediment-feeders, carnivorous and grazer adaptations (Burzin et al. 2001; Kouchinsky 2001). This community replacement is not only represented by an increase in biodiversity, but also by an increase in the abundance of preserved specimens. In the Esla nappe, it is associated with the abrupt disappearance of reef mounds and their associated archaeocyaths and the rapid immigration of diverse, lowermost Middle Cambrian, relatively cosmopolitan trilobites related to a change to more open marine conditions as shown by basinward facies shift, tectonic breakdown and drowning of the platform (see Álvaro et al. 2000b). Similar community replacements have been reported previously in neighboring platforms of the western Gondwana margin. Several lines of evidence point to a widespread biocrisis across the Lower–Middle Cambrian transition, as the culmination of a worldwide decline of trilobites and other taxa that led to a globally diachronous extinction (Debrenne 1991; Álvaro et al. 1999).

The Lower–Middle Cambrian boundary in the Iberian Peninsula represents the end of the relatively endemic, inner-platform trilobite survivors of the area, followed by an inshore immigration of more pandemic, outer-platform trilobite faunas (Álvarez et al. 2003). This event is now confirmed in the Esla nappe based on the analysis of skeletonized microfossils.

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