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Pentaradiate diploporites (Echinodermata) from the Spanish Middle Ordovician and their taxonomic significance

Diploporitos pentaradiados (Echinodermata) del Ordovícico Medio español y su interés taxonómico

Christopher R. C. PAUL & Juan Carlos GUTIÉRREZ-MARCO

Abstract: New Middle Ordovician pentaradiate diploporites from the southern Central Iberian Zone, Spain, show that *Oretanocalix* is an aristocystitid with five ambulacra; all other aristocystitid genera have 2–4 ambulacra. The oral frame is composed of eight plates, with five, facet-bearing, circumorals (**COO**) and three, non-facet-bearing, periorals (**POO**). This necessitates a new interpretation of the aristocystitid oral area. Previous interpretations assumed four COO and four POO. Weathered examples lack oral cover plates, show that CO1 and CO4 do not reach the peristome inner margin and reveal abundant diplopores covered by thin epistereom in life. Diplopores grew at plate sutures and were incorporated into both adjacent plates. The genus *Batalleria* is a sphaeronitid with food grooves that branched within the peristome. Branching reflects Lovén's law and is: AR, BL, CR, DL, ER, where A–E denote Carpenter's ambulacra and L (left) and R (right) denote on which side the first branch lies. Each branch has a separate ambulacral orifice. All other sphaeronitids have one ambulacral orifice per ambulacrum. Diagnoses of the genera *Oretanocalix* and *Batalleria*, and their type species *O. murchisoni* and *B. batalleri*, are revised. *Oretanocalix julioi* n. sp., from the Darriwilian of the Toledo Mountains, is the oldest representative of the genus.

Resumen: Se presenta nuevo material de *Oretanocalix* y *Batalleria*, dos géneros de blastozoos diploporitos pentaradiados procedentes de la Zona Centroibérica meridional española. El primero se caracteriza por tener cinco ambulacros, en vez de los 2 a 4 conocidos en el resto de los aristocistítidos, y una teca con abundantes diploporos recubiertos por un epiestereoma delgado. En su zona oral se reconocen cinco placas circumorales (**COO**, con facetas) y tres periorales (**POO**, sin facetas), pero las placas CO1 y CO4, que soportan los ambulacros D y B, respectivamente, no alcanzan el margen interno del peristoma. Ello obliga a revisar la diagnosis de la familia Aristocystitidae, pues las interpretaciones previas consideraban el área oral formada por cuatro COO y cuatro POO. Por su parte, el género *Batalleria* es un esferonítido muy particular porque presenta surcos alimentarios ramificados dentro del peristoma, siguiendo el patrón de Lovén con la fórmula AR, BL, CR, DL, ER, más un orificio ambulacral separado para cada rama. Desde el punto de vista taxonómico se revisan también las especies atribuidas a ambos géneros, estableciéndose *Oretanocalix julioi* n. sp. como la forma más antigua, procedente de lutitas del Dobrotiviense basal (Darriwiliense superior bajo) de los Montes de Toledo centrales.

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INTRODUCTION

The Ordovician echinoderm fauna of Spain includes some diverse, but sometimes poorly known diploporite blastozoans (Arroyo & Lara, 2002; Gutiérrez-Marco & Colmenar, 2011, and references therein). Here we describe new specimens of two such genera, which are unique within the families to which they belong, thus requiring modification of the diagnoses of those families as well as illuminating the evolution of diploporite blastozoans. The first, *Oretanocalix* Gutiérrez-Marco, 2000, belongs in the family Aristocystitidae, but is unique in possessing five ambulacra. Almost all other, previously described aristocystitid genera have four ambulacra, but the type genus, *Aristocystites* Barrande, 1887, has two and the only known Silurian genus, *Triamara* Tillman, 1967, has three. Typical aristocystitids have an elongate mouth with a frame composed of eight plates (Fig. 1). Paul (2017, p. 589, fig. 7) recently interpreted these as four central perioral plates and four more distal circumoral plates that bear ambulacral facets. This pattern seemed characteristic of aristocystitid genera (*e.g.*, Parsley, 1990 and Paul & Parsley, 2019 for *Aristocystites*; Makhlouf *et al.*, 2017 for *Lepidocalix* Termier & Termier, 1950a; Paul, 2017 for *Aristocystites, Calix* Rouault, 1851, *Glaphocystis* Chauvel, 1966, *Lepidocalix* and *Sinocystis* Reed, 1917; plus *Prokopius* Paul, 2018 and *Enodicalix* Paul

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& Gutiérrez-Marco, 2020). *Oretanocalix* possesses the typical, elongate peristome of aristocystitids with cover plates arranged in an outer series of larger plates and a central smaller series, but it differs from all other aristocystitids in having a fifth ambulacrum (ambulacrum A of Carpenter, 1884, 1891).

Hitherto, the only example of *Oretanocalix* that showed the external surface of the oral area was obscured in the region between the facets of ambulacra E and A. Recently discovered additional specimens reveal the complete plating of the oral area (Fig. 2). *Oretanocalix* may have five ambulacra, one more than any other aristocystitid genus known to date, but it still has only eight plates forming the mouth frame. Thus, the five facet-bearing plates are all circumoral plates (Paul, 1973, 2017). It appears that when aristocystitid genera failed to develop ambulacrum A, they retained the circumoral plate (CO3) on which it would have developed. The same thing happens in other stemless diploporites of the closely related families Holocystitidae and Sphaeronitidae. Genera such as *Trematocystis* Jaekel, 1899 (Holocystitidae) and *Tetreucystis* Bockelie, 1984 or *Diplosphaeronis* Paul, 1973 (Sphaeronitidae) have only four ambulacra, but plate CO3 is still present. Thus, a new interpretation of the oral plating in aristocystitid diploporites with five circumoral plates and only three perioral is presented herein (Figs. 1F, 2).

Another unexpected aspect of the oral plating in *Oretanocalix* is that specimens which have lost the oral cover plates reveal a very broad peristome margin in which the circumoral plates of ambulacra B and D (CO4 and CO1, respectively) do not reach the inner margin of the peristome. The plates on either side of CO1 and CO4 meet beneath these two plates and exclude them from the inner peristome margin (arrowheads, Fig. 2C). This is another example of Palaeozoic blastozoans in which ambulacra B and D differ from the other three ambulacra (see Paul, 2015, 2017; Paul & Hotchkiss, 2020). Our material suggests that in Spain *Oretanocalix* is represented by two species, *O. murchisoni* (Verneuil & Barrande, 1855), the type species and *O. julioi* n. sp. Similarly, *Batalleria* Chauvel & Meléndez, 1978 (Fig. 3A) apparently has an oral frame previously thought to be diagnostic of the family Sphaeronitidae, as well as a large madreporite-like hydropore, previously only reported in the family Aristocystitidae. *Batalleria* was originally assigned to an undetermined family and then to the Sphaeronitidae (Chauvel & Meléndez, 1986, p. 456) because it had five ambulacra, whereas at that time all aristocystitids were thought to have four or fewer ambulacra. *Batalleria*, has a pentaradiate oral

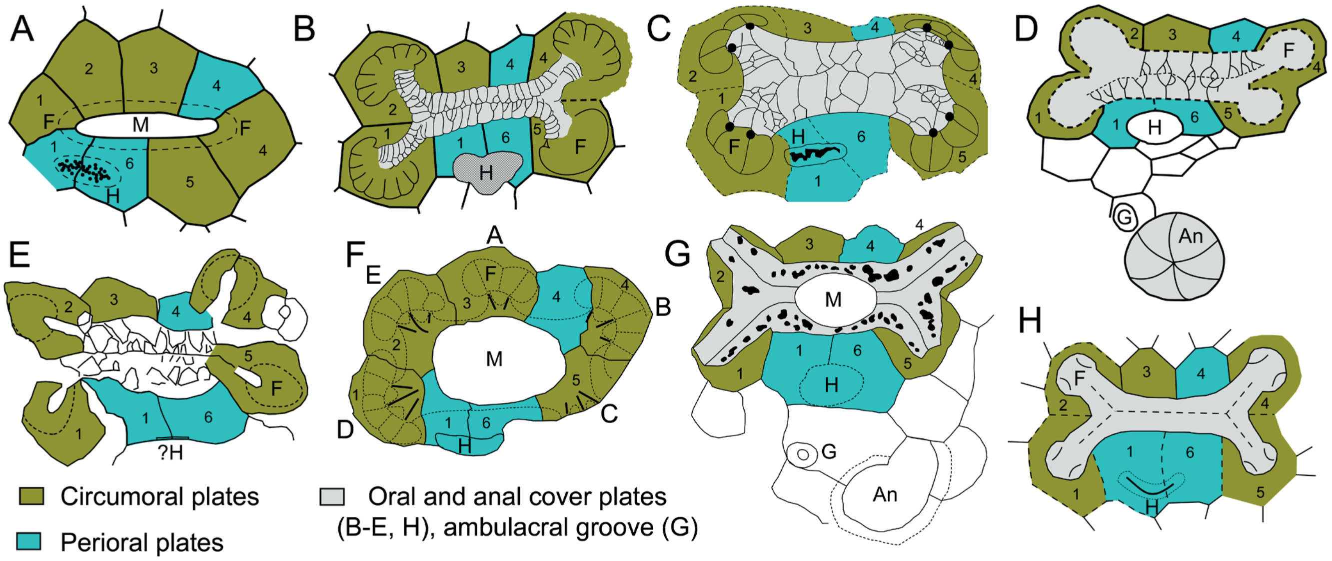


Figure 1. Idealized diagrams of the oral plating of eight genera of aristocystitid diploporites. **A,** *Aristocystites bohemicus* Barrande, 1887; **B,** *Calix sedgwicki* Rouault, 1851; **C,** *Enodicalix inornatus* (Meléndez, 1958); **D,** *Glaphocystis globulus* Chauvel, 1966; **E,** *Lepidocystis pulcher* Termier & Termier, 1950a; **F,** *Oretanocalix julioi* n. sp.; **G,** *Prokopius sculptus* (Barrande, 1887); **H,** *Sinocystis loczyi* Reed, 1917; to show elongate mouth (**M**) surrounded by eight 'oral' plates; five 'second orals' or circumorals (COO, 1–5) and three 'first orals' or perioral (POO, 1, 4, 6). Note that in *Oretanocalix* all five second oral plates bear ambulacral facets, two in ambulacrum A and three in ambulacra B–E. *Calix, Enodicalix, Prokopius* and *Glaphocystis* all have four ambulacra, but the plate in the position of ambulacrum A (second oral 3) is still present. *Aristocystites* has only two ambulacra each with a single facet at the ends of the elongate mouth, but still the same number of 'oral' plates. Plate PO1and PO6 share the hydropore (**H**), which is often a large, madreporite-like orifice. **A–E,** Ambulacra designated according to Carpenter's system (Carpenter, 1884); **An,** Anus; **G,** Gonopore; **M,** Mouth. (A) redrawn from Barrande (1887, pl. 10, fig. 15); (B) from Chauvel (1977, fig. a, p. 315); (C) modified from Paul and Gutiérrez-Marco (2020, fig. 1A); (D) from Chauvel (1966, pl. 4, fig. 1e); (E) modified from Makhlouf *et al.* (2017, fig. 6A$_2$); (F) new; (G) modified from Paul (2018, fig. 4); and (H) modified from Paul (2017, fig. 7.5). Drawings not to scale.

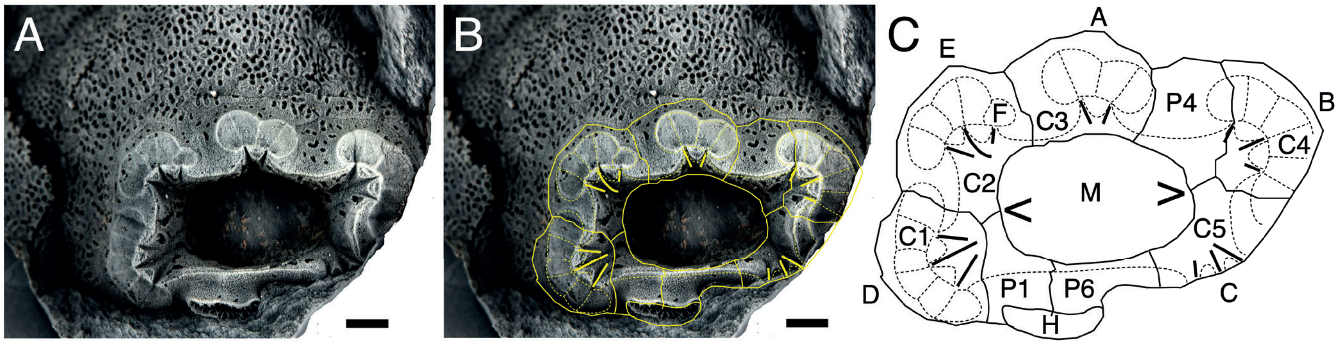


Figure 2. Oral area and plate interpretation of *Oretanocalix julioi* n. sp., lowermost Dobrotivian (*c*. lower Darriwilian 3) of Navas de Estena, Ciudad Real. Specimen DPM-A1-997-2. **A,** Latex cast of oral area, whitened with magnesium oxide; **B,** The same with interpretation of the oral plating and peristome superimposed; **C,** Interpretation of plates. **A–E,** Ambulacra A–E; **C1–C5,** Circum-oral plates; **F,** Ambulacral facet; **H,** Hydropore; **M,** Mouth; and, Periorial plates arrow heads indicate PO4:CO5 and PO1:CO2 sutures; heavy solid lines indicate food grooves, solid lines plate sutures, dashed lines outlines of peristome and facets; scale bar = 1.5 mm.

area with five ambulacra arranged in a 2-1-2 pattern (Sprinkle, 1973) and each of which branches alternately within the oral area (Fig. 3A). Its oral cover plates differ from those of all other aristocystitid and sphaeronitid genera. Regrettably, the arrangement of plates forming the peristome frame is unknown in the first specimen found (DPM-MT-208) that showed the oral area of *Batalleria batalleri* (Meléndez, 1951), the type species of *Batalleria*. Other specimens show that the oral frame of *Batalleria* was composed of six plates, five in radial positions and bearing the ambulacral facets (that is circumorals), the sixth in the CD interambulacrum and bearing the right half of the large hydropore (H, Fig. 3A). Although *Batalleria* has an oral frame diagnostic of the Sphaeronitidae (Fig. 3B, 3C), it is unique in having ambulacra that branch alternately within the peristome, each branch giving rise to its own ambulacral orifice and (presumed) brachiole facet. All other sphaeronitid genera in which the oral cover plates are known (with the exception of *Glyptosphaerites* Müller, 1854) have just six interradial cover plates, which Paul (1971, p. 7) called palatals. During growth, the number of palatal plates remained constant. Equally, no matter how much the food grooves may branch, nor how many facets there are per ambulacrum, only a single food groove enters the mouth via a single ambulacral orifice in each ambulacrum. All the branching takes place outside the limits of the peristome (Fig. 3B, 3C). Thus, *Batalleria* is unique in having ambulacra that branch within the peristome, each branch of which terminates in an individual ambulacral orifice, and in adding oral cover plates during growth. It also differs from all known sphaeronitid genera in having a large, madreporite-like hydropore. Ambulacra that branch within the peristome and add cover plates during growth plus large madreporite-like hydropores are typical of aristocystitid genera and suggest links between the two families. Finally, *Batalleria* possesses typical diplopores, but also a few fistulipore-like canals that arise in one thecal plate and terminate in an adjacent plate. At least some diplopores and all fistulipores start as a single perpendicular canal on plate sutures. In both a second perpendicular canal arises connected by an external tangential canal. In diplopores, both perpendicular canals and thus the whole diplopore become incorporated in the same thecal plate during further growth. In fistulipores, the two canals become incorporated into the two adjacent plates and the tangential canals lengthen during further growth. Thus, it requires only slight changes in the growth pattern to produce a fistulipore rather than a diplopore. Fistulipores (Paul, 1972) are characteristic of caryocystitid Rhombifera, not diploporites, and indeed Meléndez first attributed the type species, *B. batalleri*, to the caryocystitid rhombiferan genus *Echinosphaerites* (Meléndez, 1951, p. 10). *Batalleria* is also unique among diploporites in having a few fistulipore-like respiratory canals. Nevertheless, fistulipores occur in rhombic sets across all plate sutures in fistuliporites, so we do not think the presence of occasional fistulipore-like canals in *Batalleria* indicates a close relationship between fistuliporite rhombiferans and sphaeronitid diploporites. This paper redescribes the type species of both *Batalleria* and *Oretanocalix*. Both genera have widely separated peristome, gonopore and periproct and a large, madreporite-like hydropore, all features more typical of aristocystitids than of sphaeronitids.

As with the recently named genus, *Enodicalix* Paul & Gutiérrez-Marco, 2020, relevant Spanish, Ordovician taxa first described and named and therefore with taxonomic precedence, were often based on inadequate type material. Recent discoveries have improved our knowledge of the morphology of these genera, which we are attempting to re-describe to modern standards using the new specimens. Nevertheless, this requires reviewing the evidence that relates the new material that preserves key characters to the originally described type material. In turn, this should help establish with greater certainty the essential characters of members of diploporite families, such as the Aristocystitidae and Sphaeronitidae, and hence clarify their evolutionary relationships.

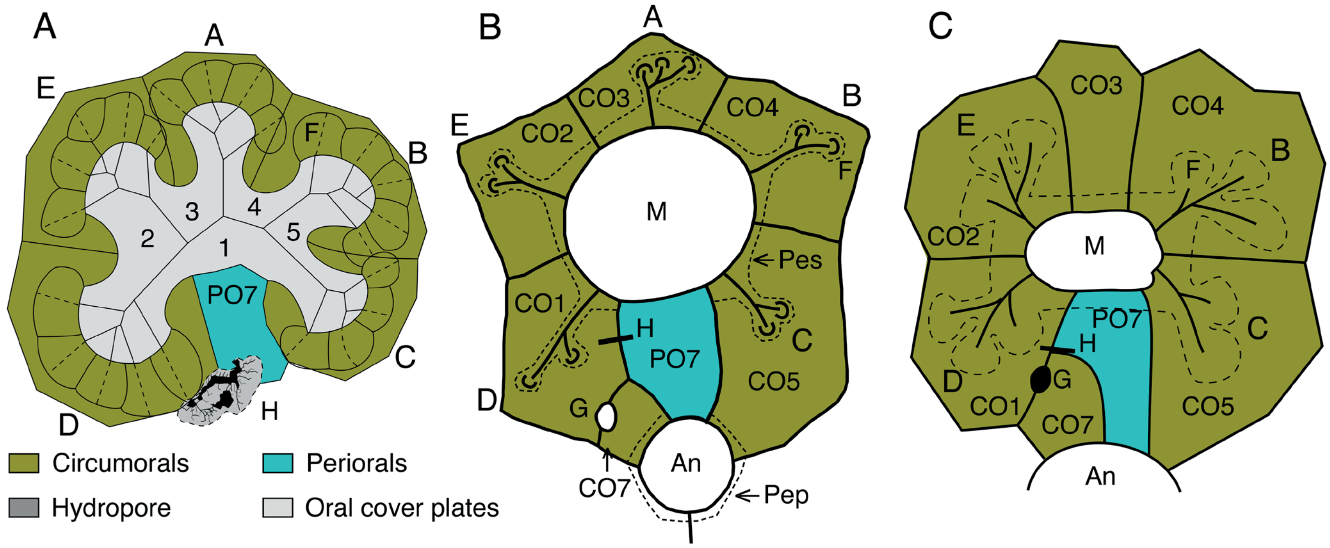


Figure 3. Idealized diagrams of the oral plating in sphaeronitid diploporites. **A,** *Batalleria* Chauvel & Meléndez, 1978; **B,** *Eucystis* Angelin, 1878; **C,** *Tetreucystis* Bockelie, 1984. All three genera have a mouth frame composed of six plates, five radial circumorals (CO1–CO5) and a sixth perioral (PO7) in the CD interradius. The mouth is usually covered by six primary oral plates (palatals) not yet found preserved in *Eucystis* and *Tetreucystis*, and apparently only five (1–5) in *Batalleria*. The hydropore (**H**) is usually a slit across the PO7:CO1 suture, but is a large madreporite-like structure in *Batalleria*. In many sphaeronitids a single plate (PO7) contributes to both the peristome (**Pes**) and periproct (**Pep**) border. Where so, the gonopore (**G**) is a circular pore across the CO7:CO1 suture. In *Batalleria* and the genera of the subfamily Glyptosphaeritinae, additional plates occur between the mouth (**M**) and anus (**An**), and the gonopore occurs in a tubercle set entirely within a single plate. *Batalleria* is unique among sphaeronitid diploporites in having ambulacra that branch within the peristome and therefore additional secondary cover plates over the mouth and multiple ambulacral orifices in each ambulacrum. In all other sphaeronitids the ambulacra branch outside the peristome and may extend beyond the circumoral circlet of plates terminating in small facets (**F**). **A–E,** Ambulacra A–E; solid lines indicate plate sutures and food grooves, dashed lines outline of the peristome with ambulacral facets and periproct. Drawings not to scale.

FOSSIL LOCALITIES, STRATIGRAPHY AND AGE

The material studied comes from several localities in the southern part of the Central Iberian Zone of the Iberian Massif, which was formed in the Variscan Orogeny (Fig. 4A). All are located towards the middle part of the Ordovician succession overlying the ubiquitous Armorican Quartzite (Lower Ordovician, essentially Floian). The Middle to lowermost Upper Ordovician rocks, collectively referred as "*Tristani* Beds" or "*Neseuretus* Shales and Sandstones" (Gutiérrez-Marco *et al.*, 2002), are predominantly composed of dark shales and siltstones with variably significant sandstone intercalations that predominate towards its upper part, ending with massive quartzites representing the lowermost Upper Ordovician strata (Fig. 4B). The remaining Upper Ordovician succession exhibits internal discontinuities on a regional scale, and is composed of alternating shales, siltstones and sandstones overlain by a thin Katian limestone (coeval with the Boda climatic event) and Hirnantian shales, sometimes replaced by glaciomarine diamictites (Gutiérrez-Marco *et al.*, 2002, 2019).

A map of the main Ordovician outcrops of the Iberian Massif with the location of the fossiliferous localities studied herein is shown in Figure 4A. The studied diploporites come from two different areas of the southern part of the Central Iberian Zone: the first corresponds to the Toledo Mountains, where the locality NE-VIIc (abbreviated as NE in Fig. 4A) is placed in the southern flank of the Navas de Estena syncline; and the second area corresponds to the Almadén and Calatrava–Viso del Marqués regions, with two fossil localities occurring respectively in the southern flank of the Almadén syncline (AL in Fig. 4A) and the northern branch of the Puertollano–Almuradiel synclinorium (CC in Fig. 4A).

From a stratigraphical point of view, the material from locality NE-VIIc in the Toledo Mountains comes from a relatively narrow interval (*c.* 15 m) of fossiliferous mudstones alternating with noduliferous siltstones, located towards the upper third of the Navas de Estena Formation. This is a thick (up to 800 m) Darriwilian succession of massive dark mudstones and siltstones, partly with noduliferous horizons. Locality NE-VIIc was first described by Gutiérrez-Marco *et al.* (1984, p. 424) as situated 4,650 m SE of the town of Navas de Estena (Ciudad Real), and can be more accurately placed *c.* 250 m to the north of the km 7 of the provincial road CR-701 (39º 28′ 2.5″ N, 4º 28′ 52.6″ W). Besides the genera *Calix*, *Phlyctocystis*, *Codiacystis* and some crinoids, cited from here by Chauvel and Meléndez (1978, 1984), Gutiérrez-Marco *et al*. (1984), Escribano Ródenas *et al*. (1999), Gil Cid and Domínguez-Alonso (2000) and Gil Cid *et al.* (1996, 1998, 2004), the locality yielded pentaradiate aristocystitids identified as *Oretanocalix* sp. by Gutiérrez-Marco (2000), and also mentioned by Gil Cid and García Rincón (2012, locality NE). These same specimens are here described as the new species *Oretanocalix julioi* n. sp., with NE-VIIc its type stratum and locality. Due to the record of some characteristic trilobites and brachiopods in the concurrent assemblage, the locality was reported by Gutiérrez-Marco (in Gutiérrez-Marco *et al*., 1984, tab. 1) and Rábano (1989) as basalmost Dobrotivian according to the Bohemo-Iberian regional scale (Gutiérrez-Marco *et al*., 2015, 2017), equivalent to a lower (but not lowermost) upper Darriwilian stage in terms of the global chronostratigraphy (Bergström *et al*., 2009).

Also in the Toledo Mountains area, lower Oretanian (*c*. middle Darriwilian) strata placed in lower beds of the same Navas de Estena Formation, include in the adjacent Algodor–Milagro syncline the type locality of *Enodicalix inornatus* (Meléndez) (VPA in Fig. 4A), whose stratigraphic position is also indicated in the left column of Figure 4B.

The next locality that supplied part of the studied material was named AL-IV in the papers of Gutiérrez-Marco *et al.* (1984, p. 424) and Chauvel and Meléndez (1986, p. 451). It is situated *c*. 8,400 m E of Almadenejos (Ciudad Real), towards the km 23 of the provincial road CR-424 (AL in Fig. 4A: 38º 44′ 26″ N, 4º 37′ 20″ W), although the fossiliferous outcrops of the same bed extend up to km 24. The latter belongs to the lower part of the Guindo Formation, a unit consisting of 30–50 m of dark shales with coquinoid beds and rare noduliferous horizons. The locality is particularly rich in diploporite remains, sometimes represented by undeformed and partly silicified specimens, so it is probably the same place as the one indicated by Verneuil and Barrande (1855) in the Almadenejos area, where Casiano del Prado collected their new taxon ‘*Echinosphaerites*’ *murchisoni*. This is a classic fossil locality for the Almadén region, although Bouyx (1962) took credit for its ‘discovery’ much later. The holotype of *Batalleria batalleri* (Meléndez, 1951) also comes from there, and among the original material collected by the French author, Chauvel and Meléndez (1978, 1984) described some aboral regions attributed to *Calix rouaulti* Chauvel, 1936, as well as new specimens of *B. batalleri*. So far, the last species is restricted to this fossil site, from where an important specimen collected by one of us (Gutiérrez-Marco in Chauvel & Meléndez, 1986, p. 456), represents a well-preserved oral fragment which will be reviewed later. Trilobites associated with the echinoderms were identified by Rábano (1989, her locality AC-II = AL-IV) and are indicative of the upper lower Dobrotivian according to the Bohemo-Iberian regional scale, equivalent to an upper (but not uppermost) upper Darriwilian stage in terms of the global chronostratigraphy (Fig. 4B).

Table 1. Size of oral area in specimens of *Oretanocalix julioi* n. sp.

Specimen	Width (mm)	Height (mm)	Ratio W:H
MGM-8555-O (Holotype)	13.5		
DPM-NE-251	16.1	10.0	1.61
DPM-NE-1007	16.2	8.8	1.91
DPM-A1-997-4	C 14	C 9	1.56
DPM-A1-997-1		8.8	
DPM-A1-997-2	13.5	8.2	1.65
MGM-8556-O		9.4	
MGM-8561-O	18.3	12.7	1.44
MGM-8557-O	17.7	10.6	1.67
MGM-2004-O	18.1	11.8	1.53
Mean	16.20	10.04	1.635

Finally, the third and last fossil locality (CC in Fig. 4A) occurs in the northern branch of the Puertollano−Almuradiel synclinorium, along the north-eastern bank of the Fresneda-I lake, from the foot of the reservoir wall to km 47,450 of the regional road CM-411. In this place a very complete and fossiliferous section of the Guindo Formation crops out (*c*. 75 m thick), overlain by up to 150 m of alternating shales and sandstones belonging to the lower member of the Botella Formation (Fig. 4B). The record of abundant shelly fossils is virtually continuous within the Guindo Formation, whose lower 30 m are correlatable with those of the locality AL-IV and also yielded trilobites representative of the upper lower Dobrotivian (= upper [but not uppermost] upper Darriwilian) according to Rábano (1989, locality CC-II). The main fossiliferous bed for diploporites corresponds to the site designated either as CC-IV (Gutiérrez-Marco *et al*., 1984; Chauvel & Meléndez, 1986) or as CC-II (Rábano, 1989) –the same place under a different name−, in 38º 37′ 0.5″ N, 3º 40′ 52″ W. From here were recorded specimens of ‘*Calix rouaulti*’ Chauvel, 1936, *Calix* aff. *segaudi* Termier & Termier, 1950b, *Phlyctocystis granulata* Chauvel, 1966, *P*. cf. *gigas* (Termier & Termier, 1950b), and *Aristocystites metroi* (Parsley & Prokop in Parsley, 1990): Chauvel and Meléndez (1984, 1986), Gutiérrez-Marco and Baeza (1996), together with *Batalleria batalleri* (second locality for the species) and the first poorly preserved representatives of *Oretanocalix murchisoni.* Higher up in the succession, the latter species becomes somewhat more frequent in the upper half of the Guindo Formation, associated with trilobites of the *Placoparia borni* Biozone, which indicates the lower upper Dobrotivian (uppermost Darriwilian to basalmost Sandbian). These horizons are documented, for example, about 600 m to the E of the reservoir wall, in 38º 36′ 60″ N, 3º 40′ 48″ W (locality CC-V). The last occurrence of *Oretanocalix murchisoni* and *Batalleria batalleri* in the studied section corresponds to a relatively thick (*c*. 3−5 m) intercalation of argillaceous shales approximately 25–30 m above the base of the lower member of the Botella Formation, which is designated as fossiliferous

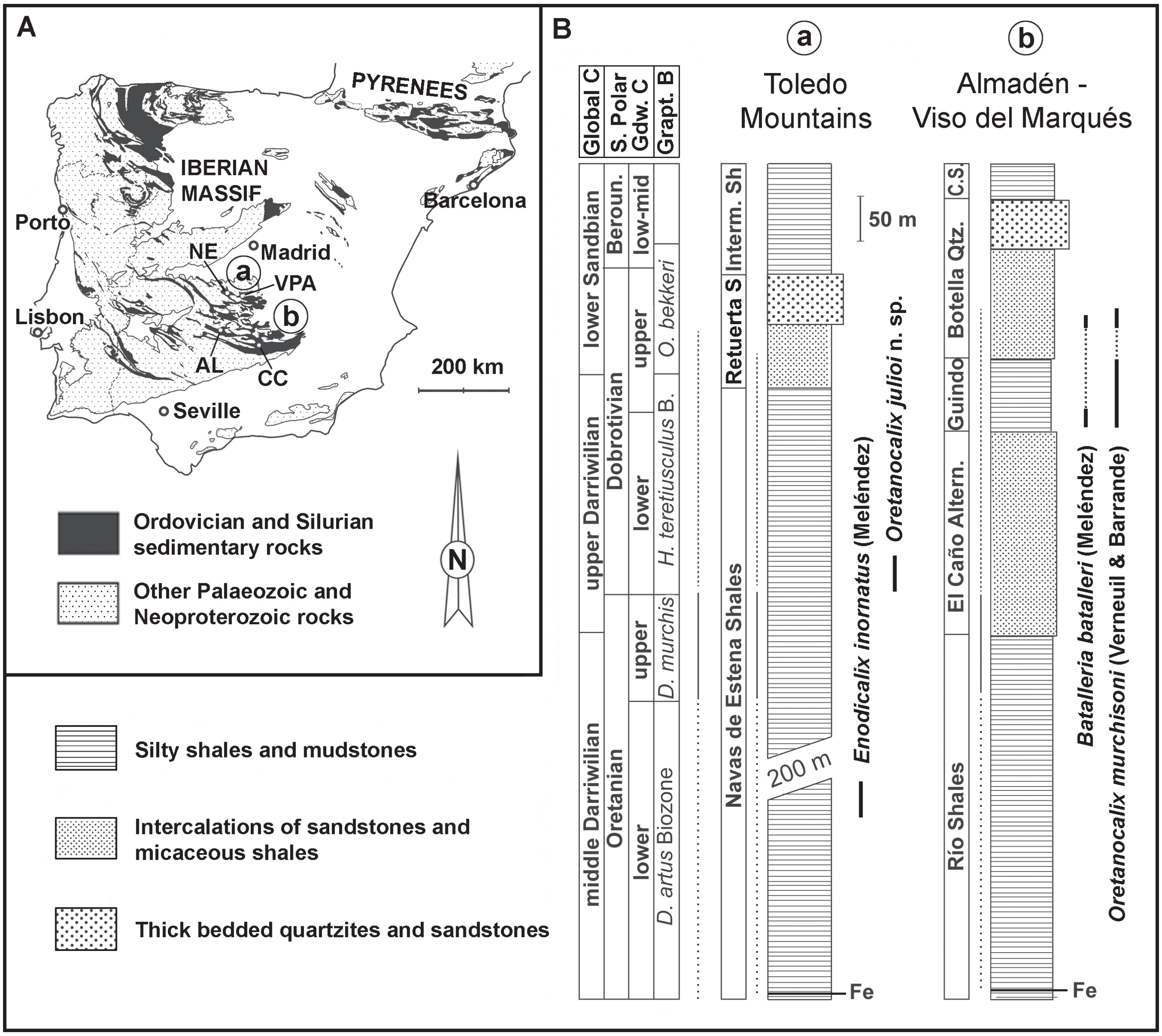


Figure 4. Stratigraphic and geographic occurrence of the studied material. **A,** Map of the main Ordovician–Silurian outcrops of the Iberian Massif, with reference to the palaeontological localities mentioned in the text. Abbreviations: **AL,** Almadén–Almadenejos; **CC,** Calzada de Calatrava–Viso del Marqués; **NE,** Navas de Estena; **VPA,** Ventas con Peña Aguilera. **a** and **b** (encircled) are the representative areas of the lithostratigraphic units detailed to the right; **B,** Stratigraphical columns of the main Middle Ordovician formations in the southeastern Central Iberian Zone (see map). The left-hand columns indicate the approximate equivalence between the global chronostratigraphy (**Global C.**), the South Polar Gondwanan regional scheme (**S. Polar Gdw. C**) and some graptolite biozones (**Grapt. B**). Other abbreviations: **Altern.**, Alternations; **B,** Biozone; **Beroun.,** Berounian; **C.S.,** Cantera Shales; ***D.,*** *Didymograptus* (and *D. murchisoni*); **Fe,** thin oolitic ironstone bed; **Guindo,** Guindo Shales; **H.,** *Hustedograptus*; **Interm. Sh.,** Intermediate Shales; ***O.,*** *Oepikograptus*, **Qtz,** Quartzite; **S,** Sandstone. Note that the stratigraphic range of the graptolite biozones are directly annotated on the left side of each column. Modified from Reyes-Abril *et al.* (2019).

bed CC-VI and crops out on the road embankment (38º 36′ 51″ N, 3º 40′ 34″ W). Most of the *O. murchisoni* specimens that preserve the oral region come from this horizon, while the aboral regions were commonly confused with '*Calix rouaulti*'. However, the bulk of the material gathered by amateur collectors comes from the extension to the west of the fossiliferous bed, which was completely excavated by the road widening works and lies under the roadway towards km 46,920. The trilobites and brachiopods recorded from CC-VI indicate that this shale intercalation clearly corresponds to the uppermost Dobrotivian (top of the *Placoparia borni* trilobite Biozone), being equivalent to the lower Sandbian (Fig. 4B) and therefore the record of *O. murchisoni* and *B. batalleri* extends into the basal Upper Ordovician.

MATERIALS AND METHODS

The specimens studied herein occur as internal, external or composite moulds occurring in argillaceous shales, affected by a variable degree of diagenetic compaction. No original calcareous material is preserved. Only very few specimens occur as natural external casts involving thecal silicification processes.

Latex casts were made from critical external moulds that preserve the details of the oral area and other features of the external surface. A replica using silicone and epoxy resin was also made in order to duplicate an important specimen of *Batalleria* for a second repository.

Latex casts and natural moulds were whitened with magnesium oxide or white fingerprint powder for photography. Measurements of diplopores and other morphological features were made using a Kyowa binocular microscope with a graticule eyepiece. Specimens were photographed using a Canon EOS 7D digital camera with Canon Macro 60 and 100 mm lens. Figures were assembled with Adobe Photoshop CS3 and CS6 Extended.

Repositories and institutional abbreviations

The new material described herein is deposited at the Museo Geominero of Madrid (**MGM**), which belongs to the Instituto Geológico y Minero de España (**IGME-CSIC**: the former Spanish Geological Survey), and where the originals of Meléndez (1951) and Gutiérrez-Marco (2000) are also preserved. The remaining illustrated material belongs to the palaeontological collection of the Department of Geodynamics, Stratigraphy and Palaeontology of the Complutense University of Madrid (**DPM**), corresponding to the papers of Chauvel and Meléndez (1978, 1984, 1986) and Gil Cid and García Rincón (2012).

SYSTEMATIC PALAEONTOLOGY

Terminology follows Paul (1973) for general diploporite morphology, and Paul (2017) for aristocystitid oral plating, except for the new interpretation of the oral frame plates introduced herein.

Class DIPLOPORITA Müller, 1854
Subclass ANAMBULACRALIA Paul & Toom, 2021

Diagnosis. Stemless diploporites with an oral frame composed of either or both radial circumorals and interradial periorals; outside the peristome food grooves lie directly on thecal plates and lack floor and cover plates.

Remarks. The Anambulacralia includes four families of directly attached diploporites; the Aristocystitidae, Holocystitidae, Sphaeronitidae and Parasphaeronitidae, if the latter is really sufficiently distinct from the Sphaeronitidae to justify a separate family. Traditionally, aristocystitids have been regarded as less closely related to the other three families and a formal superfamily Aristocystitoida has been recognized containing just the family Aristocystitidae (Makhlouf *et al*., 2017; Paul *et al*., 2019). Recognition of the homologies of aristocystitid oral plates, suggests that all four families are related, which makes the taxonomic status of any superfamily including the four families identical to that of the Anambulacralia. It seems best at the current state of knowledge to treat each family separately rather than recognize superfamilies.

The peristome is covered by a palate of (usually) six palatal plates in the Sphaeronitidae and Holocystitidae, and by a double series of cover plates in the Aristocystitidae. The peristome cover is unknown in the Parasphaeronitidae. Outside the peristome, food grooves lack both floor and cover plates and bear no constant relationship to the underlying thecal plates.

Family ARISTOCYSTITIDAE Neumayr, 1889

Diagnosis. Directly attached diploporites with elongate oral area surrounded by at least eight plates (three periorals [POO] and five circumorals [COO]), and covered by two series of larger outer and smaller central cover plates; with 2–5 ambulacra bearing 1–5 brachioles each; with a large hydropore shared by plates PO1 and PO6 and often a spout-like gonopore usually within a single plate near the periproct; with thecal plates densely covered with diplopores that are frequently sealed externally by a thin epistereom and sometimes extended into spine-like projections.

Remarks. This diagnosis differs from those given by McDermott and Paul (2019, p. 530) and Paul and Gutiérrez-Marco (2020, p. 3) in that it is now known that aristocystitids have five circumoral plates (CO1-CO5) and three periorals, PO1 and PO6, which share the hydropore, plus PO4. We retain the phrase ‘at least eight plates’ because the oral plating of the Silurian genus *Triamara* has not been established unequivocally and it may have nine oral plates.

Chauvel (1966) accepted three subfamilies within the Aristocystitidae: the Aristocystitinae, Hippocystinae and Calixinae [*sic*] (= Calicidae Termier & Termier, 1950b). The first was characterized by a variable theca, large plates and a thick thecal wall aborally, traversed by numerous canals opening externally in variable, elongate peripores, and a slit-like peristome with two facets. Only the last character is significant. Two genera were included, *Aristocystites* Barrande, 1887, and *Maghrebocystis* Chauvel, 1966, but the thecal orifices and facets are totally unknown in *Maghrebocystis*. Thus, this subfamily is in fact equivalent to the genus *Aristocystites*.

Hippocystines were characterized by pine cone or egg-shaped theca, larger adorally, tumid or strongly convex, but not tuberculate plates arranged in regular circlets aborally, variable elongate, but not oval or rounded peripores, and a peristome with four, rarely three or five, facets. Odd numbers of facets were included because the genera attributed were *Glaphocystis* Chauvel, 1966, *Holocystites s.l.*, and by implication *Hippocystis* Bather, 1919. Genuine *Holocystites* Hall, 1864 and related genera are now attributed to the separate family Holocystitidae (Paul, 1971; Frest, 1983; Sheffield & Sumrall, 2015, 2017), which removes genera with five ambulacra. *Triamara*, the only aristocystitid included within '*Holocystites*' *s.l.*, has three ambulacra, each with a pair of facets and would not be included in the Hippocystinae now. Paul and Parsley (2019) have shown that the type species of *Hippocystis* is a species of *Aristocystites s.s*. Paul (2018) proposed the new name *Prokopius* for *Hippocystis sculptus* (Barrande, 1887). This leaves just *Glaphocystis* and *Prokopius* in the Hippocystinae, both of which have just four ambulacral facets.

The Calicinae Termier & Termier, 1950b, were characterized by Chauvel (1966, p. 45) as having elongate or pyriform thecae with regular plate circlets especially in juveniles, some plates tubercular, peripores oval or sometimes rounded, a slit-like mouth bifurcated at each end and so tetraradiate. Genera included were *Calix* Rouault, 1851, *Sinocystis* Reed, 1917 and *Phlyctocystis* Chauvel, 1966. At that time the oral area of *Phlyctocystis* was entirely unknown and the characters of the oral area claimed for the Calicinae are virtually identical to those seen in the Hippocystinae. As far as number of ambulacra is concerned, one genus *Aristocystites* has just two, the only known Silurian genus, *Triamara* has three, each with a pair of facets and *Oretanocalix* has five, each with multiple facets. All the other genera in which the oral area is known have four ambulacra, but some, such as *Glaphocystis*, *Prokopius*, *Lepidocystis* and *Sinocystis* have a single facet per ambulacrum, whereas *Calix*, *Enodicalix* and *Phlyctocystis* have multiple facets. Finally, *Binocalix* McDermott & Paul, 2019, has paired facets, but the number of ambulacra is unknown. If one attempted to separate subfamilies on the number of ambulacra, then three subfamilies would have a single genus each, and all the rest would be attributed to the Calicinae. Acceptance of subfamilies must await a thorough review of the entire family.

Genus *Oretanocalix* Gutiérrez-Marco, 2000

Type species. *Echinosphaerites murchisoni* Verneuil & Barrande, 1855. Dobrotivian (= upper Darriwilian); Almadén region, Spain.

Diagnosis. Pentaradiate aristocystitids with multiple facets in each ambulacrum that were added during growth, with two internal calcified mesenteries or ridges aborally.

Remarks. *Oretanocalix* is the only aristocystitid genus with five ambulacra. Neither the taxonomic nor functional significance of the aboral internal ridges is understood at present. Taxonomically, they may occur in other calicine genera, but at present we have no evidence of this. The close association at the same locality and stratigraphic horizon of internal moulds with a pentaradiate oral area and others with internal ridges suggests that both are characteristic of *Oretanocalix*. The matching internal and external moulds of *O. murchisoni* (Fig. 5B, 5C) clearly demonstrate that specimens with internal ridges have a tuberculate aboral theca.

Gutiérrez-Marco (2000) suspected that more than one species of *Oretanocalix* existed in the Spanish Ordovician and distinguished them as *O. murchisoni* and *O.* sp. We are able to confirm this and give a description of the second species, *O. julioi* n. sp. Stratigraphically, the new species is the oldest known *Oretanocalix*, occurring the basal Dobrotivian regional stage, a partial equivalent of the Dw3 (upper) division of the international Darriwilian stage. The type species, *O. murchisoni*, is slightly younger, occurring in the topmost lower Dobrotivian and into the upper Dobrotivian, most probably reaching Upper Ordovician strata (Fig. 4B).

Occurrence. *Oretanocalix* is known from the Dobrotivian (upper Darriwilian and basal Sandbian) in Spain. Jacinto *et al.* (2014, fig. 1A) and Jacinto (2015, p. 13–14, pl. 1, figs. A–F) recorded a possible *Oretanocalix*? sp. from the middle Berounian (*c.* Sandbian 2 – Katian 1) strata of central Portugal which is the youngest known occurrence of *Oretanocalix* if genuine. Gutiérrez-Marco (2000, p. 85) and Gutiérrez-Marco *et al*. (2003, p. 158) identified as a probable *Oretanocalix* sp. the paratype '1697o' of *Calix*? *cornuta* Chauvel (Chauvel, 1978, fig. 4f), coming from the upper part of the Ouine-Inirne Formation (upper Dobrotivian; uppermost Darriwilian) of the Moroccan Anti-Atlas. It shows a pair of internal ridges that however diverge from a higher point in the aboral region than in the Iberian species described below. The record of the genus *Oretanocalix* in the Armorican Massif (western France) is currently limited to undescribed specimens found by Dominique Chauvin (Saint-Aubin-les-Châteaux) and shown in photographs. These come from lower Dobrotivian shales in the Angers Formation, at the "Paléordovi" site placed ESE of Sion-les-Mines (Loire-Atlantique).

Oretanocalix murchisoni (Verneuil & Barrande, 1855)

Figures 5, 6

v1855 *Echinosphaerites Murchisoni* n. sp.; Verneuil & Barrande, p. 995–997, pl. 26, fig. 7.

1941 *Calix murchisoni*; Chauvel, p. 76.

v1984 *Calix rouaulti* Chauvel, type specimen of *Echinosphaerites murchisoni*; Chauvel & Meléndez, p. 437, fig. 7a, pl. 4, fig. 10.

v2000 *Oretanocalix murchisoni*; Gutiérrez-Marco, p. 85, figs. 1a–1d. With full list of previous synonymies.

?2002 *Oretanocalix*? sp.; Arroyo & Lara, p. 98.
2013 *Oretanocalix murchisoni*; Lefebvre *et al*., p. 181.
2015 ‘*Calix murchisoni*’; Jacinto *et al*., p. 163, tab. 1.

Holotype. Unnumbered internal mould of an incomplete theca (aboral part) from the Verneuil collection, Centre des Sciences de la Terre, Lyon, France, refigured by Chauvel and Meléndez (1984, pl. 4, fig. 10) and by Gutiérrez-Marco (2000, fig. 1a–1d).

Type locality. Solana del Romeral near Almadenejos, Ciudad Real, Spain.

Type horizon. Guindo Formation, uppermost lower Dobrotivian regional stage, upper Darriwilian International stage.

Material. Holotype and numerous internal moulds, including some that show the oral areas with five ambulacra and the aristocystitid pattern of oral cover plates. All the latter are from the Guindo Shale Formation (CC-IV and CC-V fossiliferous beds) and lower Botella Quartzite Formation (ibidem CC-VI), upper lower to uppermost Dobrotivian (*c*. upper Darriwilian−basal Sandbian) of Calzada de Calatrava, Spain (Fig. 4).

Diagnosis. A species of *Oretanocalix* with broadly cylindrical theca, curved aborally with strongly tuberculate primary thecal plates in the aboral third of the theca.

Description. The holotype is an incomplete internal mould of a broadly cylindrical theca with a slightly curved and tapered aboral pole, which shows two internal mesenteries that were calcified in life and diverge at about 125°. The mould is about 60–70 mm high by 30–42 mm at its widest and lacks the oral area entirely. The surface of the mould is covered with internal casts of the diplopore canals especially basally. Specimen MGM-8563-O resembles the type and shows the curved aboral pole tapering to a point (Fig. 5A) with two calcified internal mesenteries (grooves on the mould). It also lacks the oral area but the cylindrical theca is larger (160 mm high by 60–65 mm in diameter). Plate sutures are difficult to determine in the aboral third of the theca, but are more obvious adorally. They belong to three generations. Matching internal and external moulds of specimen MGM-8564-O show that whereas the internal surfaces of all the thecal plates are only gently curved (Fig. 5C), in the aboral third of the theca the external surfaces of the largest plates were tuberculate (Figs. 5B and 6C). All plates were penetrated by numerous perpendicular canals of diplopores (Figs. 5E−5G and 6C).

The most complete specimen is an internal mould of a juvenile theca which lacks the tapered aboral pole, is almost cylindrical and approximately four times as high as wide (Fig. 6D).

Other internal moulds show that the peristome had all five ambulacra and typical aristocystitid oral cover plates (Fig. 5E). Impressions of the stone canal leading to the hydropore (s, Fig. 5E), gonopore (g, Fig. 5E) and anal pyramid (An, Fig. 5E) are also preserved. The anal pyramid had 5–7 anal plates as well as pits between the plates for muscles or ligaments to close the anal pyramid (Fig. 5D). Aborally, the two internal mesenteries were connected (Fig. 5F). They usually diverge at a considerable angle (about 75° in MGM-8567-O, Fig. 5F), but rarely are nearly parallel (specimen MGM-8568-O, Fig. 5G). In the latter, the mesenteries diverge adorally (arrow in Fig. 5G). Neither the biological, nor taxonomic significance of these differences is understood.

Occurrence. The species ‘*Calix murchisoni* Verneuil & Barrande’ has been cited from a number of Middle Ordovician localities in the Central Iberian Zone of Spain and Portugal, as well as in the West Asturian-Leonese Zone (NW Iberian Massif) and the Iberian Cordillera (NE Spain): references in Gutiérrez-Marco (2000) and Arroyo and Lara (2002). Also, it has been mentioned (as ‘*Echinosphaerites Murchisoni*’) in the French Armorican Massif (Tromelin & Lebesconte, 1876a, tab. D, no. 79, 1876b, tab. C, no. 79; Oehlert, 1882, p. 37). However, none of these citations was accompanied by description and illustration of particular specimens and their relation with *Oretanocalix* remains speculative.

Lebesconte (comment on the reprinted version of Rouault, 1878/1883, p. 44 and explanation to pl. 16) considered ‘*Calix murchisoni*’ as being equivalent to the fifth morphotype of *C. sedgwicki*, that Rouault differentiated under the name ‘Corythe forme Ibérienne’ (= ‘Iberian thecal morph’). In the same paper, Rouault (1878/1883, pl. 16, fig. 1) redrew the holotype of *E. murchisoni*, proposing a reconstruction of its external appearance (his pl. 16, fig. 1a –without aboral tuberculiferous plates) plus an internal view including the plating and a longitudinal section of a thick theca with a large and protruding basal tubercle (his pl. 16, fig. 1b). These details are based on the imagination of that author.

Initially, Chauvel (1941, p. 77) also considered the holotype of *C. murchisoni* as related with his ‘morphotype γ’ of *Calix sedgwicki* Rouault, 1851, but later (Chauvel, 1980, p. 5) placed it close to the morphotypes ‘d’ or ‘f’ of *Calix rouaulti* Chauvel, 1936. According to Chauvel (1980, p. 5) the ‘insufficient preservation’ of the holotype of *C. murchisoni* prevented application of the taxonomic priority of the Spanish species over the subsequently-proposed forms (either *C. rouaulti* or even *C. sedgwicki*). The only exception to this attribution was that of Meléndez and Chauvel (1983, p. 152), who briefly accepted the species as ‘*Calyx* [sic] *murchisoni*’. Chauvel and Meléndez (1984) mentioned it again but within the supposedly wide polymorphism of *C. rouaulti*. The relationships between *O. murchisoni* and the poorly defined *C. rouaulti* will not be clarified until the discovery of complete specimens attributable to this second species, which show the

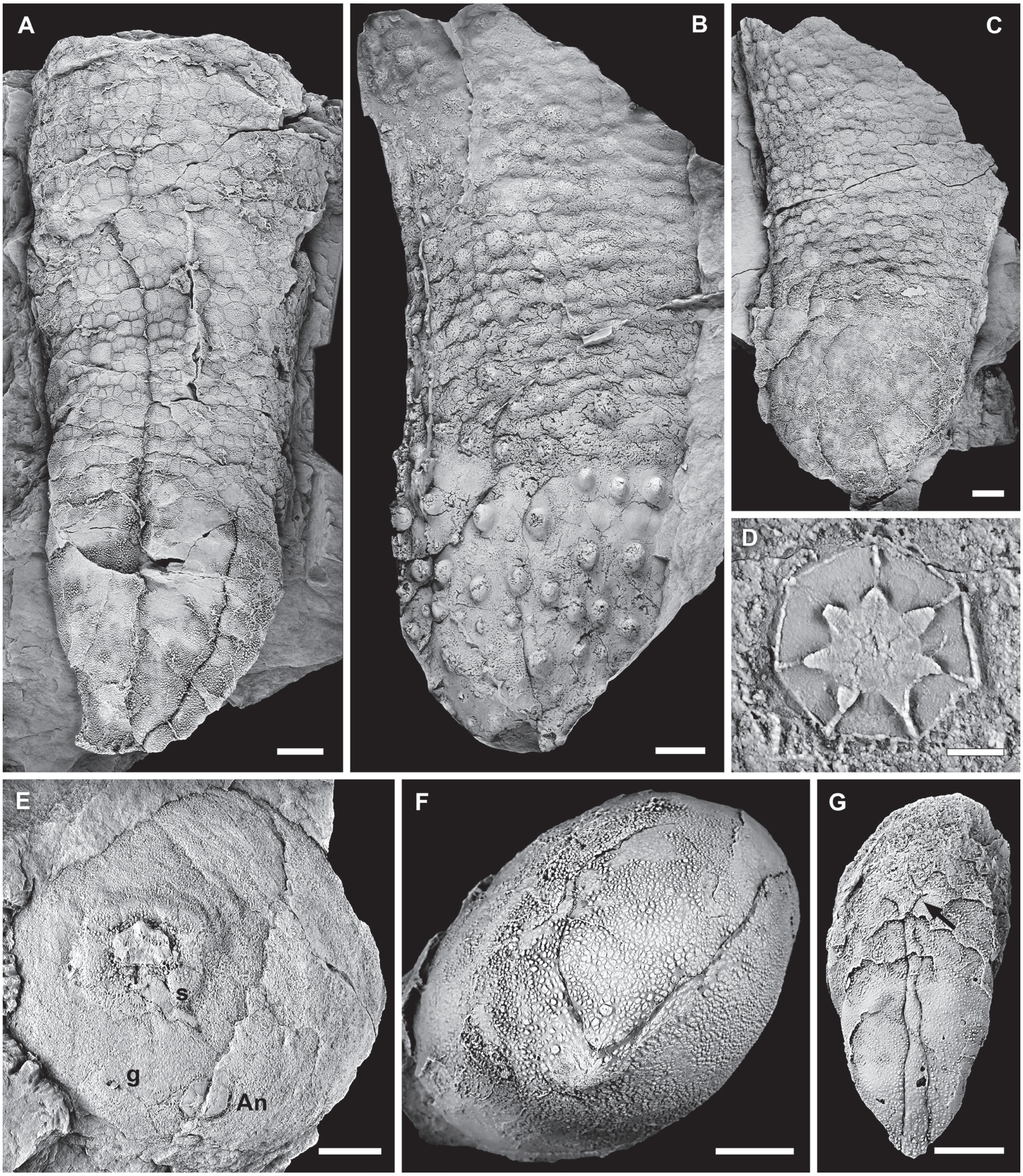


Figure 5. *Oretanocalix murchisoni* (Verneuil & Barrande, 1855), from the Dobrotivian strata (*ca*. upper Darriwilian−basal Sandbian) of Calzada de Calatrava, Spain. **A,** Internal mould of specimen MGM-8563-O from locality CC-V, showing two internal ridges (grooves on the mould) extending from the base of the theca; **B–C,** Specimen MGM-8564-O, also from CC-V; **B,** Latex cast of the external mould showing circlets of plates bearing tubercles aborally; **C,** Natural internal mould showing abundance of thecal plates which are smooth aborally; **D,** Detail of anal pyramid on natural internal mould of specimen MGM-8565-O, with seven anal plates, from locality CC-VI; **E,** Natural internal mould of specimen MGM-8566-O from locality CC-V, showing pentaradiate oral area, stone canal (**s**), gonopore (**g**) and anus (**An**). **F,** Aboral view of internal mould of specimen MGM-8567-O from locality CC-IV, to show the two internal ridges diverging at an angle of about 75 degrees; **G,** Lateral view of internal mould of specimen MGM-8568-O from locality CC-IV, showing the two internal ridges almost parallel and diverging orally (arrow head); scale bars = 10 mm, except D = 3 mm.

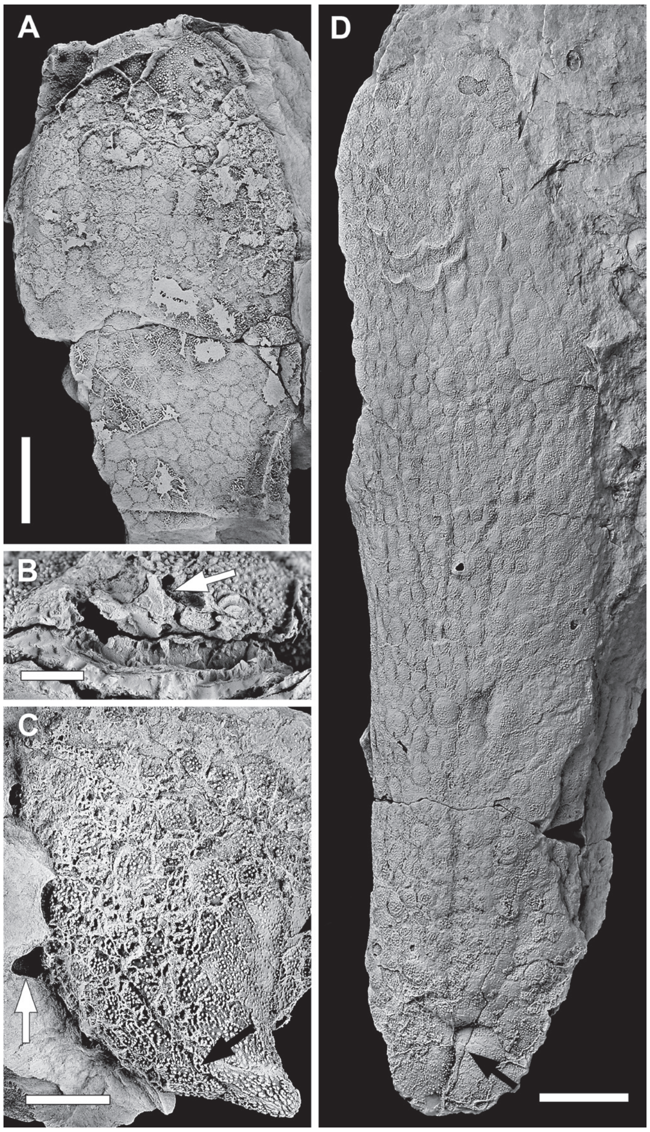


Figure 6. *Oretanocalix murchisoni* (Verneuil & Barrande, 1855), from locality CC-VI (uppermost Dobrotivian, *c.* basal Sandbian) of Calzada de Calatrava, Spain. **A–B,** Internal mould of specimen MGM-8569-O; **A,** Fragment of a laterally compressed theca showing contours of plates and a flattened oral end; **B,** Detail of the crushed pentaradiate mouth with ambulacrum A in the middle (arrowed); **C,** Internal mould of specimen MGM-8570-O laterally preserved in matrix, showing the curvature of the aboral end, one of the two internal ridges (the groove indicated by a black arrow) and the cross section of a tuberculiferous plate (white arrow); **D,** Internal mould of specimen MGM-8571-O corresponding to a cylindrical and very elongate, almost complete juvenile theca. The black arrow indicates the groove corresponding to one of the internal ridges; scale bars = 20 mm (A, D), 10 mm (C) and 5 mm (B).

prominent aboral tuberculiferous plates combined with the tetraradiate oral area typical of the genus *Calix*.
Based on the available data, the occurrence of *Oretanocalix murchisoni* has only been confirmed in the Dobrotivian strata (upper Darriwilian to basal Sandbian) of the southern Central Iberian Zone of Spain (Almadén and Calatrava–Viso del Marqués regions).

Oretanocalix julioi n. sp.

Figures 1F, 2, 7–9

?1978 *Calix* aff. *rouaulti*; Chauvel & Meléndez, p. 78–79, pl. 1, figs. 4–5.
?p1984 *Calix inornatus*; Chauvel & Meléndez, p. 431, fig. 2a; pl. 1, figs. 6–8.
?p1984 *Calix* sp. A; Chauvel & Meléndez, p. 434, fig. 4a, ?5a–5b; pl. 3, figs. 12–13.
p1984 *Calix* sp.; Chauvel & Meléndez, p. 434–435, fig. 2c; pl. 2, fig. 7.
p1984 *Phlyctocystis* cf. *gigas*; Chauvel & Meléndez, p. 436, pl. 3, fig. 7.
?p1984 Diploporite indet. genus *T-4*; Chauvel & Meléndez, p. 436–437, fig. 6; pl. 3, figs. 9–11.
v2000 *Oretanocalix* sp.; Gutiérrez-Marco, p. 85, figs. 1e–1f.
?2002 *Oretanocalix* sp.; Arroyo & Lara, p. 98 (= *Calix* aff. *rouaulti* of Chauvel & Meléndez, 1978).
?p2002 *Oretanocalix* sp. 2.; Arroyo & Lara, p. 98 (= Genus *T-4* of Chauvel & Meléndez, 1984).
v2002 *Oretanocalix* sp. 3.; Arroyo & Lara, p. 98 (= *Calix* sp. A + *Calix* sp. –oral zones pro parte– of Chauvel & Meléndez, 1984).
vp2012 pentaradial diploporite (*Oretanocalix*); Gil Cid & García Rincón, p. 183, figs. 2.1?, 2.2; 5A–5B, 5C? [non figs. 2.3, 5D and 5G–5D? = *Batalleria batalleri*].
v2022 *Oretanocalix* sp.; Paul, p. 471−472, fig. 3.

Etymology. The species is dedicated to the Spanish geologist Julio Martín Sánchez, fieldwork partner and friend of the second author for more than 40 years.

Holotype. Specimen MGM-8555-O, an almost complete, but crushed external mould of the theca (Figs. 7A–7C).

Type locality. Navas de Estena, Ciudad Real province, Toledo Mountains region, Spain (39º 28′ 2.5″ N, 4º 28′ 52.6″ W).

Type horizon. Navas de Estena Formation, shales of the basal lower Dobrotivian regional stage, upper Darriwilian International stage.

Material. Holotype and several other external moulds showing the oral areas with five ambulacra and the aristocystitid pattern of oral cover plates, as well as internal moulds. All from the Navas de Estena Shales Formation, locality NE-VIIc (Fig. 4). Reposited paratypes: DPM-2004-O (= Gutiérrez-Marco, 2000, fig. 1e), MGM-8556-O to MGM-8562-O; DPM-A1-997-1 to DPM-A1-997-4; DPM-NE-101, 251, 1007 and 1008 (material Gil Cid & García Rincón, 2012); DPM-MT-166, DPM-MT-191 and DPM-MT-197 (material Chauvel & Meléndez, 1984).

Diagnosis. A species of *Oretanocalix* with cylindrical theca, with smooth, gently convex thecal plates all of which entirely lack tubercles.

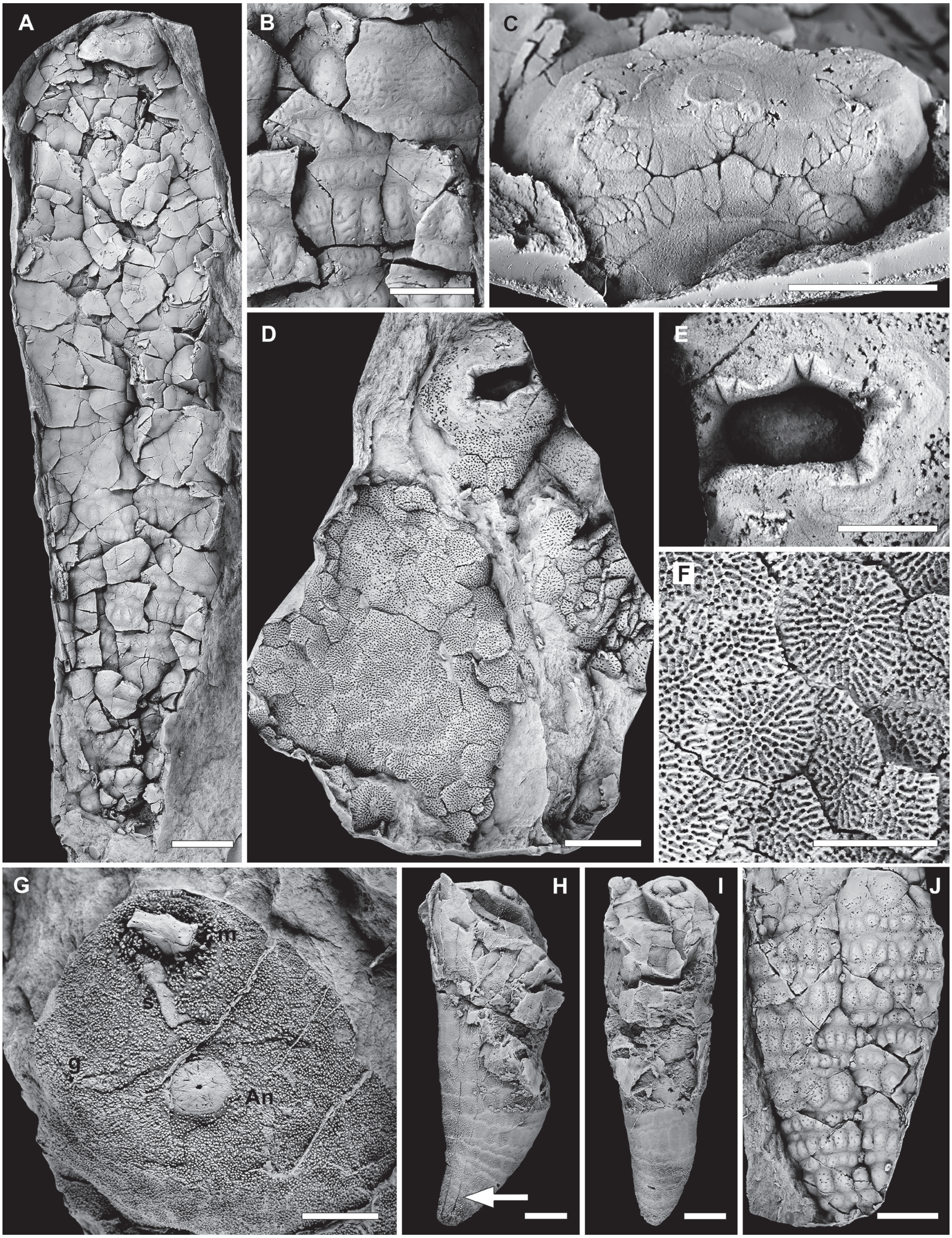
Description. The holotype is the most complete theca among the new material (specimen MGM-8555-O, Fig. 7A) is cylindrical, about 140 mm long by a maximum width of 36 mm and crushed. Another large specimen (DPM-A1-997-1) is incomplete, at least 70 by 35 mm and lacks cover plates, but reveals abundant diplopores (Fig. 7D, 7F). Specimen MGM-8555-O preserves a distorted and somewhat disarticulated attachment area aborally, about 15−16 mm diameter and part of the oral surface, which tapers rapidly from about 24 mm across to 15 mm by the peristome. The theca is crushed and some plates appear broken, but they are all entirely smooth and clearly arranged in circlets of at least three generations, which are more obvious aborally (Fig. 7A below). Plates of the aboral half of the theca are slightly tumid making the plate circlets more obvious; those in the oral half are flat. This specimen shows only the faintest trace of diplopores externally (Fig. 7B).

The oral surface of the holotype MGM-8555-O (Figs. 7C and 8) preserves the peristome, which is 13.5 mm across from the outer edge of the facets in ambulacra B and E (Tab. 1), and shows the five ambulacra characteristic of *Oretanocalix* in a 2-1-2 pattern, as well as the arrangement of cover plates typical of aristocystitids. Six large cover plates reach from the outer edge of the peristome to the midline suture (1–6, Fig. 8C) two in the posterior CD interambulacrum and one each in the other four interambulacra. One of the two in the CD interambulacrum is larger, central and directly opposite the suture between cover plates leading to the A ambulacrum. Each ambulacrum terminates in multiple facets (F, Fig. 8C), up to 2 mm across. Only those in ambulacrum A show well, where there are two, a large and a small developing facet to the right about 0.85 mm across at maximum. Ambulacrum B had three facets and E at least two, the facets of ambulacra C and D are not preserved. Specimen MGM-8556-O shows three facets in ambulacrum C, whereas MGM-8557-O (Fig. 9C) shows all five ambulacra with a formula of A2, B3, C3, D3, E3 apparently (Tab. 2).

The oral frame was composed of eight plates, as in all other aristocystitid genera where the number has been determined (Fig. 2C). Five oral frame plates (C1-C5 in Fig. 2C) are centred on the ambulacral grooves and largely covered by the facets for presumed brachioles. The arrangement of oral frame plates shows best on specimens that have lost their oral cover plates, such as specimen DPM-A1-997-2 (Fig. 2). Starting at the hydropore (H, Fig. 2C) and working clockwise around the mouth the following plates can be identified: PO1, CO1, CO2, CO3, PO4, CO4, CO5, PO6. The circumoral plates support the ambulacral facets and ambulacra D, E and A are immediately adjacent to each other. Plates PO1 and CO2 meet within the edge of the peristome (left arrowhead, Fig. 2C), so that plate CO1, which supports ambulacrum D, does not reach the inner edge of the peristome. Between ambulacra A and B is a single perioral plate PO4, which also meets CO5 within the peristome margin (right arrowhead, Fig. 2C), so that plate CO4, which supports ambulacrum B, also does not reach the inner edge of the peristome. Finally, plate CO5 supports ambulacrum C and has a common suture with CO4. This structure of the oral frame is unique among blastozoans and may have been characteristic of aristocystitids, but too few are known in which the oral cover plates are missing so that the details of the peristome margin can be determined. Internal moulds show that the oral frame penetrated well into the thecal cavity. In internal moulds of the theca, the oral area is raised above the surrounding oral surface from which it is separated by a moat-like groove (Figs. 7G and 9A–9B). Chauvel and Meléndez (1984, p. 431, fig. 2a) likened this to a 'donjon', the raised central keep of a Norman castle, and it is characteristic of *Oretanocalix* and other calicine aristocystitids, such as *Enodicalix* Paul & Gutiérrez-Marco (2020, fig. 4c–4d). The hydropore (h, Figs. 2C and 9D, 9F) is shared by PO1 and PO6. It is a large, complex structure composed of numerous ridges and grooves, developed in a crudely trilobed raised tubercle (Fig. 9D, 9F). Specimen DPM-A1-997-3 is the only external mould to preserve the gonopore (g, Fig. 9F) and an external view of the periproct (Pe, Fig. 9F). The gonopore is a

Figure on next page

Figure 7. Latexes and internal moulds of *Oretanocalix julioi* n. sp. to show morphology and preservation. All from the basal Dobrotivian shales (upper Darriwilian) of Navas de Estena, Spain, locality NE-VIIc. **A–C,** Holotype, specimen MGM-8555-O; **A,** Latex cast of complete but crushed specimen with epitheca preserved, to show cylindrical theca and circlets of smooth, slightly tumid plates aborally; **B,** Detail of aboral plating to show three generations of plates and traces of diplopores; **C,** View of oral area showing elongate peristome with five ambulacra and typical aristocystitid oral cover plates; **D–F,** Paratype, specimen DPM-A1-997-1; **D,** General view of entire theca showing diplopores resembling those of *Phlyctocystis* Chauvel, 1966; a worn theca lacking oral cover plates and with exposed diplopores; **E,** Detail of the oral area, ambulacral facets and food grooves; **F,** Detail of diplopores to show axes predominantly perpendicular to plate sutures; **G,** Internal mould of paratype, specimen MGM-8558-O, showing mouth (**m**), stone canal (**s**), gonopore (**g**) and anus (**An**) with six anal cover plates, and multiple casts of perpendicular canals of diplopores; **H–I,** Internal mould of paratype, specimen DPM-MT-166 (= '*Calix* sp. A' of Chauvel and Meléndez, 1984, pl. 3, figs. 12–13), showing general thecal shape, circlets of plates and traces of internal ridges (grooves on the mould) aborally (white arrow); **H,** Lateral view; **I,** Lateral view perpendicular to that in H; **J,** Latex cast of paratype, specimen DPM-MT-191 (= '*Phyctocystis* cf. *gigas'* of Chauvel and Meléndez, 1984, pl. 3, fig. 7), showing well-developed circlets of tumid plates in three generations; scale bars = 10 mm (A, D, G–J) and 5 mm (B, C, E, F).


A
B
C
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J

Table 2. Number of ambulacral branches in each ambulacrum of specimens of *Oretanocalix julioi* n. sp., with the evidence. **AO**, ambulacral orifices; **F**, facets; **FG**, food grooves.

Specimen	A	B	C	D	E
MGM-2004-O	2 AO	3 AO	3 AO	3 AO	
DPM-NE-251	2 F	3 AO	3 F	3 F	
DPM-NE-1007	2 AO	3 FG	3 FG	2? AO	
DPM-A1-997-4	2 FG	3 FG	3? FG	3 FG	3 FG
DPM-A1-997-1	2 FG	2? FG	2 FG		3 FG
DPM-A1-997-2	2 F	3 F	3 FG	3 F	3F
DPM-A1-997-3			>1 F	>1 F	2 F
MGM-8555-O (Holotype)	2 F	3 AO			
MGM-8556-O	2? F	3 F	3 F		
MGM-8561-O	1 F	2F	3? F	2 F	2 F
MGM-8557-O	2 F	3 F	3 F	3 F	3 F

distinctly pentagonal hole about 0.7 mm across, set in a raised, circular tubercle about 1.5 mm in diameter and apparently developed entirely within a single thecal plate. Specimen DPM-A1-997-3 is disarticulated so distances cannot be measured accurately, but as preserved the gonopore is about 11 mm from the centre of the hydropore and at least 7 mm from the centre of the periproct. The latter is covered by a strongly domed, hexagonal, anal pyramid composed of six plates and is about 6 mm in diameter.

External surfaces of thecal plates are smooth when unabraded (Figs. 7A–7B and 9C, 9D, 9F), but both internal moulds and worn specimens that have lost their oral cover plates show that all plates were penetrated by diplopores (Figs. 7D, 7F, 7G and 9A, 9B, 9E). The plates reach up to 6.5 mm across at their widest and the diplopores are arranged perpendicular to plate sutures (Fig. 7F). Diplopores have deep peripores the average length of which does not exceed 0.75 mm (Tab. 3) with perpendicular canals about 0.2 mm in maximum diameter at each end (Fig. 7F).

Stratigraphic and geographic range. All known specimens come from the Navas de Estena Shales Formation, lowermost Dobrotivian (= lower upper Darriwilian global stage) of the Toledo Mountains, Spain.

Remarks. The type species of *Oretanocalix* Gutiérrez-Marco, *Echinosphaerites murchisoni* Verneuil & Barrande, is based on an incomplete internal mould currently in the 'Centre des Sciences de la Terre', Lyon, France. The key characters that distinguished the genus were the presence of two calcified internal mesenteries and the oral area that showed undoubted affinities with the family Aristocystitidae, but had five ambulacra. The recognition of the genus *Oretanocalix* was a major improvement in our understanding. The internal mesenteries were previously thought to be confined to *Echinosphaerites*, a rhombiferan blastozoan, yet the holotype of *O. murchisoni* clearly bears diplopores. Secondly, up to the description of *Oretanocalix* no aristocystitid was known to possess five ambulacra. More than one species of *Oretanocalix* was thought to be present in the Dobrotivian (= upper Darriwilian–basal Sandbian) of the Central Iberian Zone, because other internal and external moulds showed oral areas with five ambulacra and typical aristocystitid oral cover plates. These are here described as *Oretanocalix julioi* n. sp.

The new species adds considerably to our knowledge of the morphology of the genus. The oral area is elongate perpendicular to the oro-anal axis, as in typical aristocystitids, but shows five ambulacra in a 2-1-2 pattern (see Sprinkle, 1973, p. 43, fig. 16). The cover plates are best seen in specimen MGM-8555-O where they are arranged in a double series on either side with broadly larger outer plates and smaller, often triangular central plates (Figs. 7C and 8). Six larger cover plates can be identified that extend from the outer edge of the peristome to the median suture, two in the CD interradius and one each in the other four interradii (1–6 in specimen MGM-2004-O, Fig. 7C). The larger of the posterior pair is central in the CD interradius and directly opposite the suture leading to the A ambulacral facets. The smaller plate is to the left, but still reaches all the way across the posterior half of the peristome. It seems highly likely that these largest cover plates

Figure 8. Oral cover plates in *Oretanocalix julioi* n. sp., from the basal Dobrotivian shales (upper Darriwilian) of Navas de Estena, Spain, locality NE-VIIc. **A,** Oral view of latex cast of holotype specimen MGM-8555-O; **B,** The same with outlines of oral cover plates indicated; **C,** Line drawing of cover plates (shaded). 1–6, primary oral cover plates; **F,** outline of facet in ambulacrum A; scale bar = 2 mm.

Table 3. Measurements of the length and width of 20 diplopores per specimen of *Oretanocalix julioi* n. sp., with mean, standard deviation (**SD**) and coefficient of variation (**CV**).

Specimen	Mean Length (mm)	SD (mm)	CV %	Mean width (mm)	SD (mm)	CV %
DPM-NE-251	0.733	0.128	17.477	0.208	0.28	13.597
DPM-A1-997-1	0.664	0.097	14.586	0.176	0.026	14.895
DPM-A1-997-2	0.634	0.104	16.404	0.169	0.023	13.488
DPM-A1-997-4	0.515	0.065	12.596	0.193	0.029	15.251
MGM-8555-O (Holotype)	0.548	0.078	14.279	0.116	0.019	16.025
MGM-8561-O	0.835	0.169	20.223	0.236	0.049	20.735

were the first secreted and so are primary oral cover plates. It is unlikely to be coincidence that the entire peristome in the two most closely related families, Holocystitidae and Sphaeronitidae, is covered by a palate (Paul, 1971, p. 6, fig. 1a, 1e) of six plates, two in the posterior interradius and one each in the other four interradii, and the suture between the posterior pair is usually offset slightly to the left of the anterior suture.

The median sutures of the oral cover plates align with the brachiole facets and sometimes the small ambulacral orifices are clearly seen. At least three of the new specimens show small facets added to the right in different ambulacra. Specimens MGM-8555-O (Fig. 8A–8C) and DPM-NE-251 show such developing facets in ambulacrum A, whereas specimen DPM-A1-997-2 shows one in ambulacrum E (Fig. 2A–2C) as well as a slightly smaller facet on the right in ambulacrum A. This shows that new feeding structures were added during growth. A single specimen each of *Calix* and *Glaphocystis* are the only aristocystitids in which the feeding structures are known. In both they are biserial brachioles and it is assumed the same was true for all aristocystitids. In *Oretanocalix* the number of facets increased during growth (Tab. 2), whereas in *Enodicalix* Paul & Gutiérrez-Marco (2020, p. 2) there always appear to have been two per ambulacrum. Nevertheless, as far as can be determined, all specimens seen so far have one less facet developed in ambulacrum A compared with the other ambulacra (Tab. 2).

The plates that form the oral frame can be detected (Fig. 2) and reveal an unexpected arrangement that requires modification of the diagnosis of the entire family Aristocystitidae. Five plates bear ambulacral facets and here are accepted as the five circumoral plates (Fig. 2C). Plates CO1–CO3 have common sutures, so that ambulacra D, E and A form a trivium. The next plate clockwise is PO4 and then plates CO4 and CO5 have a common suture, so that ambulacra B and C form a bivium. Finally, in the CD interradius are the two perioral plates (PO1 and PO6) that share the hydropore (H, Fig. 2C). In addition, specimen DPM-A1-997-2 shows that the two plates on either side of CO1 and CO4 meet adorally so that these two circumoral plates do not reach the inner margin of the peristome. This is totally unexpected, but probably results from the evolutionary process by which a triradiate ancestor developed into a pentaradiate echinoderm (Paul & Hotchkiss, 2020).

The radial arrangement of the diplopores enables us to interpret their growth. Specimen DPM-A1-997-1 (Fig. 7F) shows that newly formed diplopores arise at plate sutures and become incorporated into one of the adjacent plates. This gives rise to a pattern in which the axis of the diplopore, which connects the two perpendicular canals, is consistently orientated perpendicular to the nearest plate suture. In *Oretanocalix* the entire thecal surface is covered with diplopores, so during growth they were equally frequently assimilated into both adjacent plates. In the sphaeronitid genus *Glyptosphaerites*, diplopores were preferentially assimilated into one or other of the plates adjacent to any plate suture (Paul & Toom, 2021, p. 234).

Finally, the new specimens show variations in their preservation. The original example showing the oral plating, MGM-2004-O (Gutiérrez-Marco, 2000, fig. 1e) and specimen MGM-8555-O (Figs. 7C and 8A–8C) have all oral cover plates in place and the thecal plates appear entirely smooth externally (Figs. 7A–7B and 9C, 9D, 9F). Nevertheless, in DPM-NE-251 there is a small area where the theca has been worn and the diplopores begin to show (right in Fig. 9D). Specimen DPM-NE-1008 is also important in this context even though it is poorly preserved. It shows the oral cover plates but one or two have been lost adjacent to the ambulacral facets. These areas reveal the prominent food grooves within the peristome. This, in turn confirms that specimens DPM-A1-997-1 (Fig. 7D–7E) and DPM-A1-997-2 (Fig. 2A), which have lost all the oral cover plates and show thecal surfaces that are covered with exposed diplopores, are conspecific with *O. julioi* n. sp. At first sight specimens MGM-8555-O and DPM-A1-997-1 or DPM-A1-997-2 look very different. This, in turn, enables us to suggest that other examples previously illustrated from the same locality and horizon, such as the *Phlyctocystis* cf. *gigas* of Chauvel and Meléndez (1984, pl. 3, fig. 7) may well also be examples of *Oretanocalix*, but lack the critical oral area to confirm these suggestions. However, the arrangement of its several circles of small plates and their differences in size and morphology are quite similar in the partially disarticulated holotype of *O. julioi* and the cited specimen of `*P*. cf. *gigas*', refigured here on Figure 7J. In both cases cycles of relatively larger and elongated plates can be distinguished, which have a central bulge rather than a protruding tubercle.

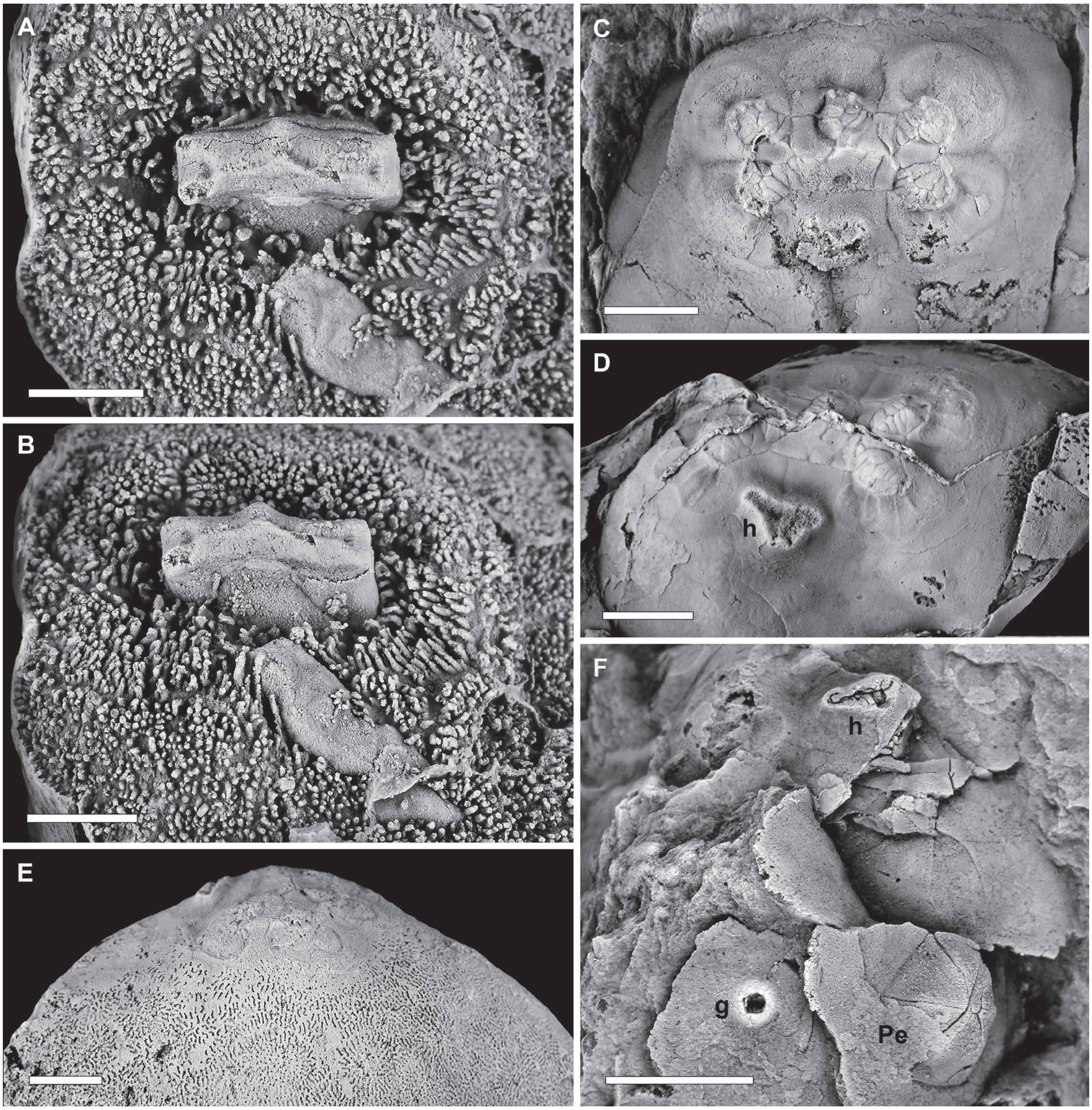


Figure 9. Details of Internal mould (**A**−**B**) and latexes (**C**−**F**) of *Oretanocalix julioi* n. sp. to show main thecal orifices and preservation. All from the basal Dobrotivian shales (upper Darriwilian) of Navas de Estena, Spain, locality NE-VIIc. **A–B,** Internal mould of specimen DPM-NE-101 showing the pentaradiate mouth surrounded by a moat-like groove leading to the formation of a 'donjon' rising deeply from the thecal cavity, and best seen in the slightly oblique view in **B**. The smooth, elongated structure near the mouth is the stone canal; **C,** Oral area of specimen MGM-8557-O showing an ambulacral formula of A2, B3, C3, D3, E3 and the hydropore; **D,** Oblique posterior view of specimen DPM-NE-251 showing the trilobed hydropore (**h**); **E,** Lateral view of the oral area of specimen MGM-8559-O, to show no distinctive relief of the mouth (seen from the B−C interambulacrum) compared with its preservation in the internal mould. The hydropore in this view is to the left from the mouth. The epitheca has been eroded showing abundant diplopores; **F,** Specimen DPM-A1-997-3, a disarticulated theca showing the hydropore (**h**), gonopore (**g**) and anal pyramid (**Pe**); scale bars = 5 mm.

Unlike *O. julioi*, in *O. murchisoni* specimen MGM-8564-O (Fig. 5B–5C) preserves matching internal and external moulds. Aborally, the internal mould (Fig. 5C) shows the characteristic pair of internal ridges and plate boundaries are less obvious aborally. The external mould (Fig. 5B) shows that the aboral theca included circlets of tubercular plates, previously regarded as characteristic of the genus *Calix*. The matching moulds show clearly that the tubercles were solid, apart from the diplopore canals. It seems likely that they were an adaptation to anchor the aboral theca more securely against currents. The smoother internal surface aborally is part of the same adaptation and results from the plates being thickened internally.

Family SPHAERONITIDAE Neumayr, 1889

Diagnosis. Anambulacralians with the mouth frame formed by five radial circumoral plates (CO1–CO5) plus plate PO7 in the CD interradius; with narrow epithecal food grooves that entirely lack flooring and cover plates, that may be developed extensively across the theca and end in multiple ambulacral facets; hydropore usually a slit-like orifice across the PO6:CO1 suture; with diplopores.

Remarks. This diagnosis differs from some recent examples (Frest *et al*., 2011, p. 60) because the significance of the epithecal food grooves that lack both flooring or cover plates was not fully appreciated previously.

Genus *Batalleria* Chauvel & Meléndez, 1978.

Type species. *Echinosphaerites batalleri* Meléndez, 1951. Dobrotivian (= upper Darriwilian); Almadenejos, Spain.

Diagnosis. Pentaradiate sphaeronitids with food grooves that divide within the peristome, thus giving six primary oral cover plates (palatals) and multiple secondary cover plates. Multiple facets in each ambulacrum added during growth, with each facet opposite a separate ambulacral orifice. Large, madreporite-like hydropore and pore structures typically diplopores, but some canals cross plate sutures and resemble fistulipores.

Remarks. *Batalleria* is unique among sphaeronitid diploporites because it has food grooves that divide within the peristome and so each ambulacral facet has its own separate ambulacral orifice. Furthermore, at each division of the food grooves a new oral cover plate was added. Five primary oral cover plates (palatals of Paul, 1971) can be recognized and several secondary cover plates occur in each ambulacrum. All other sphaeronitid genera have food grooves that leave (or enter) the peristome at a single orifice per ambulacrum and, if the food grooves branch, all branches are outside the peristome. This is even true of the 'Herpetocystinae' of Frest (1983) and Frest and Strimple (in Frest *et al*., 2011, p. 62), which are characterized by a pair of food grooves per ambulacrum, but each pair enters the peristome through a single ambulacral orifice. Typical sphaeronitids have a small, slit-like hydropore across the PO7:CO1 suture in the CD interradius. *Batalleria* has a large, madreporite-like hydropore in the same position, that is more typical of the hydropore in aristocystitid diploporites. Indeed, *Batalleria* differs so fundamentally from all other sphaeronitid genera that it may well justify the erection of a separate family of its own. Nevertheless, the construction of the oral frame is confined to the family Sphaeronitidae, so *Batalleria* shows closer affinities with that family than with any other diploporite family.

Batalleria batalleri (Meléndez, 1951)

Figures 3A, 10–13

v1951 *Echinosphaerites batalleri* n. sp.; Meléndez, p. 8–11, figs. 2, 3, text-fig. 4.
v1978 *Batalleria batalleri*; Chauvel & Meléndez, p. 81–82, pl. 2, fig. 8, text-fig. 7.
v1983 *Batalleria batalleri*; Meléndez & Chauvel, p. 154.
v1984 *Batalleria batalleri*; Gutiérrez-Marco, tab. 1.
v1986 *Batalleria batalleri*; Chauvel & Meléndez, p. 456–458, pl. 2, figs. 1–2, 5–6, text-fig. 3.
1990 *Batalleria batalleri*; Parsley, p. 285.
v2002 *Batalleria batalleri*; Arroyo & Lara, p. 98.
vp2012 pentaradial diploporite (*Oretanocalix*); Gil Cid & García Rincón, p. 183, figs. 2.3, 5D and 5G−5H? [non figs. 2.1?, 2.2; 5A−5B, 5C? = *Oretanocalix julioi* n. sp.].
v?2014 *Batalleria*? sp.; Gutiérrez-Marco *et al*., p. 31, fig. 3h.
2020 *Batalleria*? sp.; Paul & Hotchkiss, fig. 10, p. 1098.

Material. Holotype, (MGM-330-O) a fairly complete internal mould on which some original test remains, from Almadenejos, Ciudad Real, Spain, and eight thecae and partial theca preserved as external moulds, including an oral area undeformed and rather well preserved (topotype DPM-MT-208 from Chauvel & Meléndez, 1986; replica of same MGM-208O-R). New material includes specimens from Calzada de Calatrava, Ciudad Real (MGM-8572-O from locality CC-IV and MGM-8573-O and MGM-8574-O from locality CC-VI). All are from the uppermost middle to upper Dobrotivian (uppermost Darriwilian–basal Sandbian) of the southern Central Iberian Zone, Spain. A latex cast from the external mould of the specimen MGM-8572-O was illustrated by Gil Cid and García Rincón (2012, figs. 2.3 and 5D) as erroneously coming from the 'Dobrotivian of Navas de Estena (Toledo)' –*sic*−. This oral region was found in the Guindo Formation of Calzada de Calatrava (Ciudad Real), and the latex was taken from the original belonging at that time to the collection of Juan Castell Bustamante, an amateur palaeontologist living in Viso del Marqués (Ciudad Real). We identified this specimen as *B. batalleri*, and it was recently donated by the collector's widow to the Geominero Museum. The details of the peristome are illustrated here in Figures 12 and 13 (to compare with fig. 5D of Gil Cid and García Rincón, 2012). *Batalleria batalleri* remains unknown in the Toledo Mountains.

Description. The holotype (MGM-330-O; Fig. 10A–10E) is an almost complete internal mould of an ovoid theca about 95 mm long by about 55 mm maximum width showing many plates arranged in circlets of three generations (Fig. 10A mid and upper right) and all

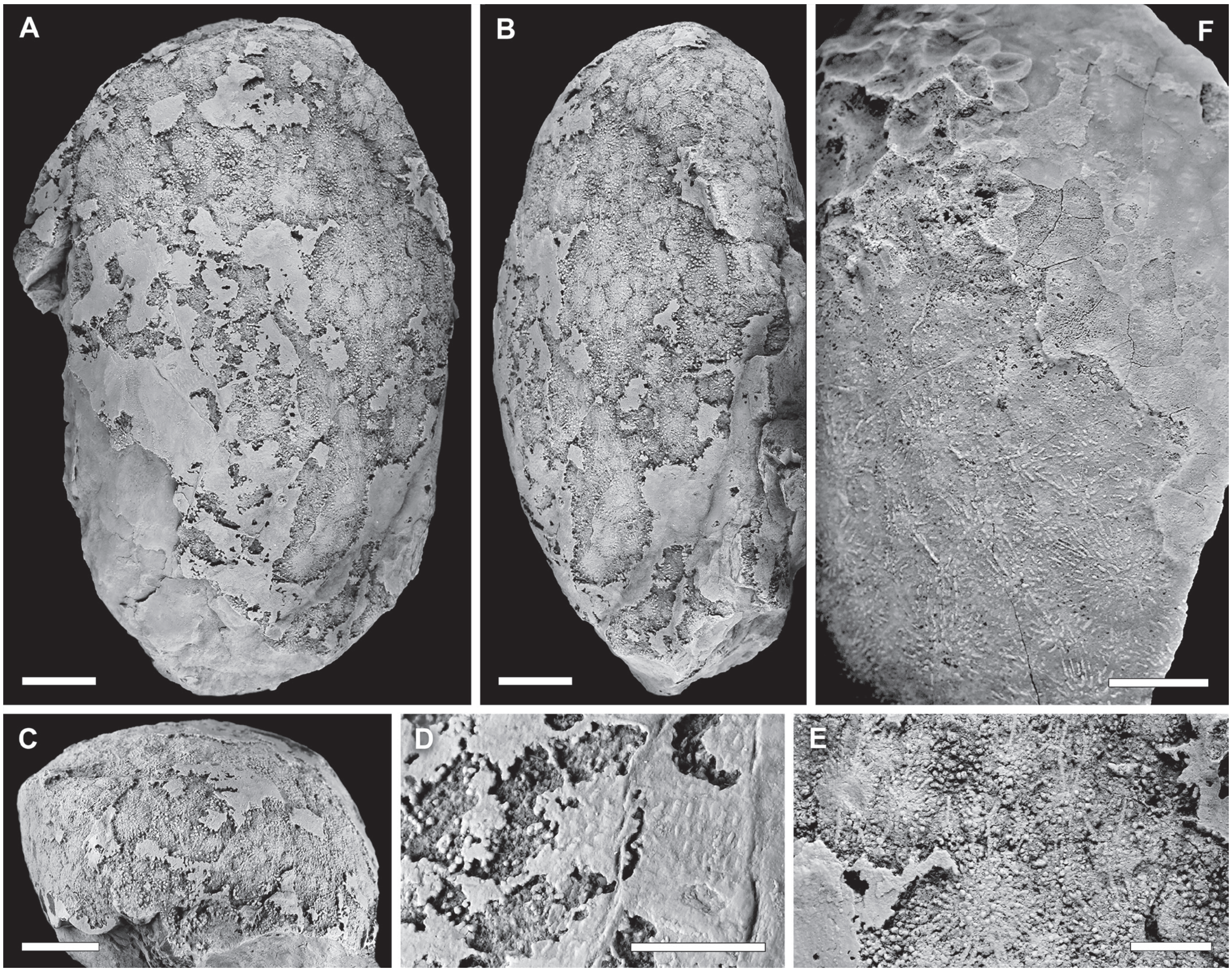


Figure 10. *Batalleria batalleri* (Meléndez, 1951), from the upper lower Dobrotivian (upper Darriwilian) of Almadenejos, Ciudad Real, Spain. **A–E,** Holotype MGM-330-O, an internal mould in lateral views (**A**, **B**) plus a terminal, probably aboral, view (**C**); **D,** Detail of the external surface of the theca where a number of small diplopores are preserved (centre right); **E,** Detail of internal mould showing casts of perpendicular canals of diplopores and of occasional long, fistulipore-like tangential canals that pass from one plate to the next; **F,** Latex cast of topotype specimen DPM-MT-208, showing typical diplopores and fistulipore-like canals plus an oblique view of the oral area (upper left); scale bars = 10 mm (A–C), 5 mm (D–F).

covered with casts of the perpendicular canals of the diplopores, but also showing the occasional canals that cross plate sutures characteristic of the genus *Batalleria* (Fig. 10E–10F). Locally, quite large areas of the smooth external surface of the plates are preserved (*e.g.*, Fig. 10A, lower left) and show traces of the diplopores as regular oval impressions about 0.5 mm long (Fig. 10D). Many diplopores appear to be subparallel to the length of the theca (Fig. 10D, right). The better-preserved end of the theca appears to be the aboral end; certainly, no trace of the oral structures is visible (Fig. 10C).

Previously available material includes specimen DPM-MT-208 (Figs. 10F, 11) illustrated and described by Chauvel and Meléndez (1986, p. 456, text-fig. 3, pl. 2, fig. 2), which preserves the oral area. This shows that the oral part of the theca was gently rounded with a definite oral platform (Fig. 11A). The five ambulacra each have multiple facets, although the details are poorly preserved in ambulacra B and C (right Fig. 11C). Each facet is set opposite a pear-shaped ambulacral orifice, with ambulacra D, E and A having 5, 5 and 4 facets, respectively (Fig. 11B–11C). The triangular hydropore (H, Fig. 11C) is close to the posterior margin of the peristome, which is covered by at least five, large primary oral cover plates (palatals), with a possible sixth close to the D ambulacrum (lower left, Fig. 11C). The adoral part of the anal pyramid (AP Fig. 11A, 11B) is just preserved on the lower margin of the specimen. It consisted of a prominent pyramid of triangular plates. Over the surface of the theca are casts of perpendicular canals of the diplopores as well as the tangential canals that cross from one plate to another and resemble fistulipores (Fig. 10F lower half).

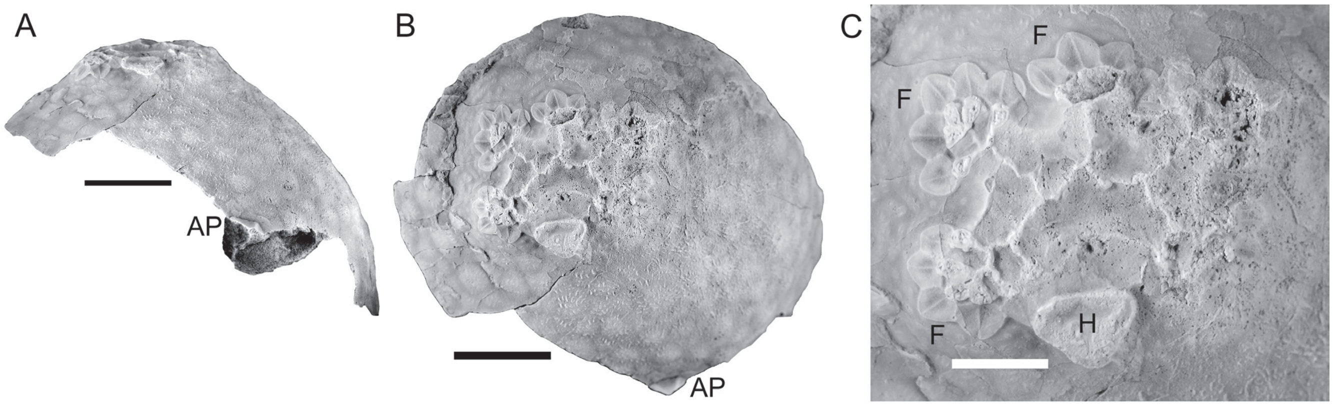


Figure 11. Natural external mould of *Batalleria batalleri* (Meléndez, 1951), specimen DPM-MT-208, upper lower Dobrotivian (upper Darriwilian), Almadenejos, Ciudad Real, Spain. **A,** Lateral view to show thecal outline, protruding oral area (top) and part of the anal pyramid (**AP**) well separated from the oral area; **B,** Oral view showing cover plates over mouth, well-preserved ambulacral facets (left), triangular hydropore and originally prominent anal pyramid; **C,** Detail of the oral area showing the ambulacral facets (**F**), large primary oral cover plates and hydropore (**H**); scale bars = 10 mm (A, B) and 5 mm (C).

New material includes MGM-8572-O, a large theca (Figs. 12–13) showing a slightly raised oral area (Fig. 12C), including the hydropore and gonopore (h and g, respectively, Fig. 12A). This specimen shows the five ambulacra clearly in a 2-1-2 pattern (A–E, Fig. 13B). Each has multiple facets, with a formula of A4, B5, C5, D5, E5. They branch within the peristome in a pattern that shows the first lateral branch alternating to the left or right of each ambulacrum as viewed in the direction of growth. This pattern is A right, B left, C right, D left, E right (Fig. 13B), which coincides exactly with Lovén's Law (Lovén, 1874) if it is stated to identify the first ambulacral plate to form and using Carpenter's ambulacral notation (Carpenter, 1884, 1891; see Paul & Hotchkiss, 2020). The primary oral cover plates are separated by the ambulacral sutures. There appear to be only five, with no trace of a suture line within the CD interambulacrum. Additional oral cover plates lie between each subsequent branch of the ambulacra (Figs. 12B and 13B). Sutures between the five circum-oral plates can be detected except that between ambulacra D and E (broken line to left Fig. 13B, 13D, 13E). The sixth oral frame plates, PO7 can also be made out and adorally shares part of the hydropore (Fig. 13E). The hydropore is an irregularly-shaped pit with many grooves set within a prominent rim (Figs. 12B and 13A, 13B, 13E). The gonopore is set within a prominent tubercle apparently within a single plate as no plate sutures can be detected crossing the tubercle (Fig. 12D). The overall thecal surface appears to have been originally smooth, but is now wrinkled due to post mortem crushing and weathering that has partially revealed the diplopores (Fig. 12D).

The internal mould of the previous specimen (Fig. 13C), as well as a second internal mould, MGM-8573-O (Fig. 13F), show that the oral area in *Batalleria* lacks the cylindrical lining penetrating deep into the theca that characterizes internal moulds of *Oretanocalix* (*e.g.*, Figs. 5E, 7G, and 9A−9B).

Discussion. The presence of long, fistulipore-like, thecal canals was a defining character of the original diagnosis of the genus *Batalleria*, so we are able to associate the external mould of the oral area of DPM-MT-208 with the original type material. Both come from the same locality and horizon. Fistulipores are exothecal canals that open internally and through which body fluids flowed in life (Paul, 1972, p. 2). They arise in one thecal plate, cross a plate suture and terminate in an adjacent plate. Normally, they are arranged in rhombic sets and are characteristic of fistuliporite rhombiferans (Paul, 1972, p. 25). Thus, it is surprising to find similar canals in a diploporite. Diplopores are also exothecal canals with two perpendicular canals connected by a tangential canal (Paul, 1972, p. 5). They differ from fistulipores primarily in being confined to a single thecal plate and in many the functional external exchange surface was composed of soft tissue and is not preserved. Nevertheless, *Oretanocalix*, among other aristocystitids certainly had calcified diplopores in life (Figs. 7A−7B and 9C−9D). It is not certain whether diplopores could arise by resorption of already existing thecal plate material, but this may have been unnecessary anyway. Epispires are single canals that pass through the theca at plate sutures. Diplopores could easily have arisen if the single perpendicular canal of an epispire became enclosed within a plate as the plate grew, but maintained a canal near the external surface, and developed a second perpendicular canal at the plate suture to connect with the tangential canal. In effect, the two epispire canals would become the perpendicular canals of a diplopore with the tangential canal between them and all enclosed within a single plate. If diplopores arose in this manner, then the axes connecting the perpendicular canals would be at right angles to plate sutures. This is exactly what we see in the diplopores of *Oretanocalix* (Fig. 7D, 7F) and to a lesser extent in *Batalleria* (Fig. 10F). A fistulipore-like canal could arise if the perpendicular canals of

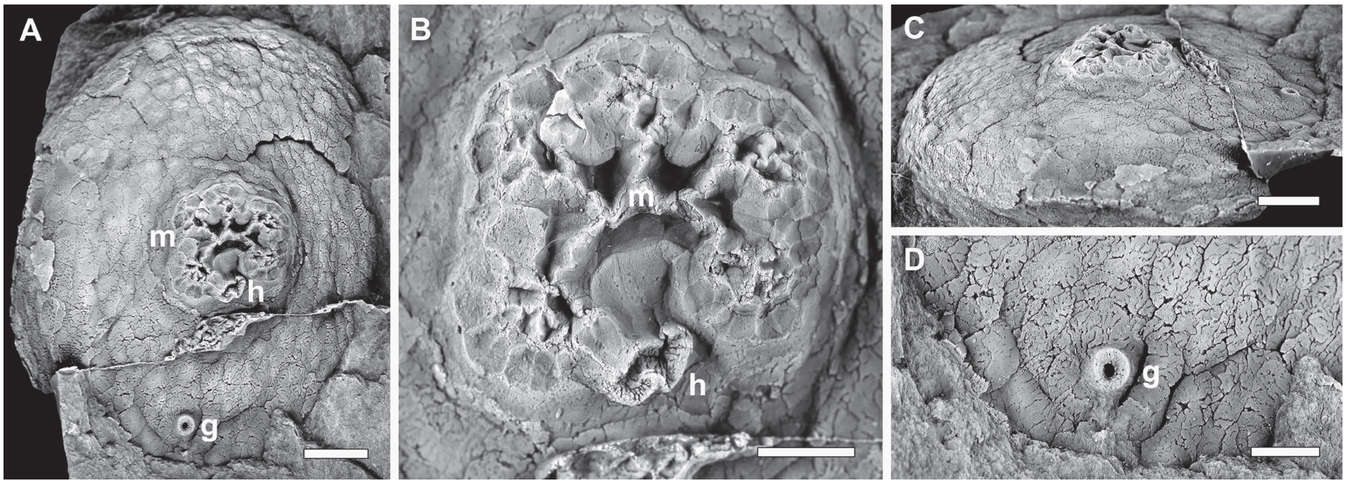
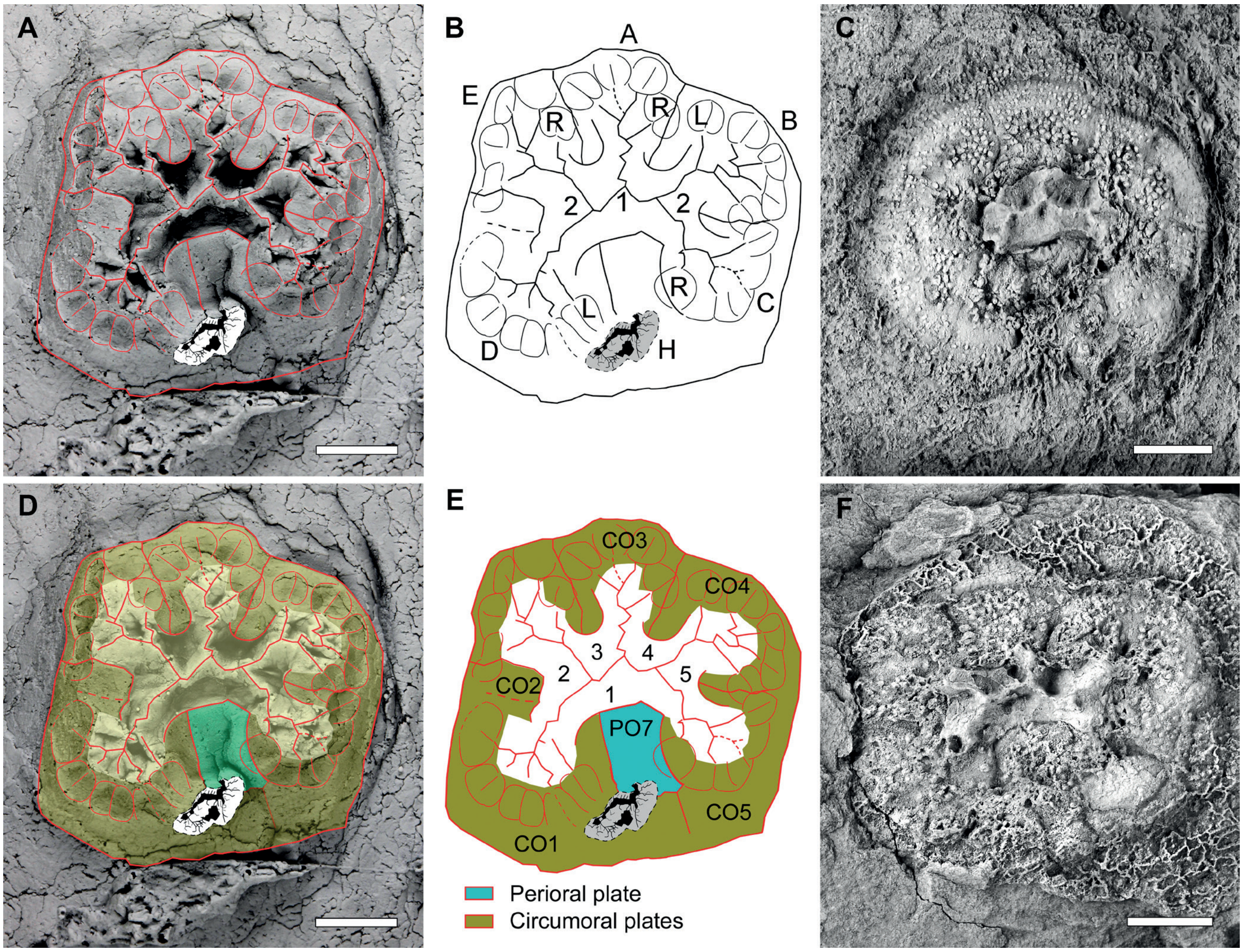


Figure 12. *Batalleria batalleri* (Meléndez, 1951), latex cast of specimen MGM-8572-O from the upper lower Dobrotivian (*c.* upper Darriwilian) of Calzada de Calatrava, Ciudad Real, Spain, locality CC-IV. **A,** General view of oral area showing mouth (**m**), gonopore (**g**) and hydropore (**h**); **B,** Detail of the oral area with five ambulacra surrounding the mouth (**m**), each with multiple facets and large, madreporite-like hydropore (**h**); **C,** Oblique oral view to show raised oral platform; **D,** Detail of the gonopore tubercle; scale bars = 10 mm (A, C) and 5 mm (B, D).



two connected epispires became incorporated in the plates on either side of the suture at which they started to develop. Clearly, the fistulipore-like canals of *Batalleria* are not arranged in rhombic sets, they are all isolated and only rarely does more than one cross any single suture (Fig. 10A−10B, 10F). Thus, we do not think the presence of occasional fistulipore-like canals indicates any close connection between *Batalleria* and fistuliporites, but rather than this is another exceptional character of the genus *Batalleria*.

CONCLUDING REMARKS

The genus *Oretanocalix* shares many characters with other aristocystitid diploporites, but differs in having all five ambulacra developed. All other aristocystitids have four or fewer ambulacra. It is also one of the earliest known aristocystitid diploporites, occurring in the Darriwilian. All genera of the related anambulacralian families Sphaeronitidae, Holocystitidae and Parasphaeronitidae have five or four ambulacra. Genera with four ambulacra always lack ambulacrum A. In sphaeronitids and parasphaeronitids the earliest known occurrence of genera with four ambulacra is Katian. Holocystitids with four ambulacra are exclusively Silurian. So, from both a stratigraphic and morphological perspective, the occurrence of five ambulacra in *Oretanocalix* could be a plesiomorphic character within the family Aristocystitidae. The superficially similar sphaeronitid genus *Batalleria* is unique within its family in having ambulacra that branch within the peristome. This is highly significant in that it implies food grooves extended beneath the oral cover plates towards a small central mouth on a soft tissue oral surface. No other diploporite preserves evidence of such a feature. Nevertheless, in sphaeronitid and holocystitid diploporites the peristome is often more than 10 mm wide, yet the functional ambulacral orifices by which food enters the peristome are a fraction of a mm wide. Why should these diploporites have needed such a wide peristome to swallow such small food particles? We are of the opinion that probably all diploporites with a large peristome covered by a palate probably had a similar oral surface beneath the cover plates leading to a small central mouth.

Supplementary information. New taxonomic name proposed in this paper, and the nomenclatural acts it contains, has been registered in ZooBank, the online registration system for the ICZN: http://zoobank.org/References/a2cf8b95-6a6b-4b59-9135-56fc200f268b

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Figure 13. *Batalleria batalleri* (Meléndez, 1951), detail of the oral area of specimens MGM-8572-O (**A**−**E**) and MGM-8573-O (**F**), respectively from the upper lower Dobrotivian (CC-IV, *c.* upper Darriwilian) and uppermost Dobrotivian (CC-VI, lower Sandbian) of Calzada de Calatrava, Ciudad Real, Spain. **A,** Latex cast of the same view as in Figure 12B with the hydropore highlighted and outlines of the oral cover plates and ambulacral facets superimposed; **B,** Interpretation of the ambulacral branching. The five ambulacra (**A**−**E**) are arranged in a 2-1-2 pattern (central branches). Then the first branches to the ambulacral facets as viewed along each ambulacrum from the centre of the mouth at (**1**) are to the right in ambulacrum A, left in B, right in C, left in D and right in E. This pattern coincides exactly with Lovén's Law in echinoids, if stated as the position of the first formed ambulacral plate in each ambulacrum (see Paul & Hotchkiss, 2020); **C,** Internal mould of the same specimen showing five ambulacra, lack of a 'donjon' style peristome and sutures between circumoral plates; **D,** Same view of the latex cast of the external mould with the hydropore highlighted and outlines of the oral frame plates and ambulacral facets superimposed; **E,** Interpretation of the oral frame plates. The mouth is surrounded by five, radial, circumoral plates (CO1-CO5), with a sixth, inter-radial perioral plate (PO7). Compare with C and F. The hydropore is shared by plates PO7 and CO1, as well as other plates posteriorly, the details of which cannot be determined. 1−5 primary oral cover plates. There is no evidence of a suture in the posterior interambulacrum; **F,** Internal mould of the oral area of a different specimen showing suture between circumoral plates; scale bars = 5 mm.

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