The diploporite blastozoan *Lepidocalix pulcher* from the Middle Ordovician of northern Algeria: Taxonomic revision and palaeoecological implications

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We present revision of the taxonomy and palaeoecology of the Ordovicían aristocystitid *Lepidocalix pulcher* from the Zaouïa of Stita (Great Kabylia, Algeria). An emended diagnosis is proposed, highlighting the four-fold ambulacral system and the typical thecal plating organised in circlets. *Lepidocalix* is here assigned to the subfamily Calicinae of the family Aristocystitidae. The latex casts show fitted sutures between plates, slightly abraded spines, and well-preserved oral surface. The thecal plates possess up to three dipores, each, included into the spines. The presence of such covered diplopores would have reduced the respiration rate, by restricting their exchange surface area. The spines covering the dipores are not articulated and they could have a protective role. *Lepidocalix* is interpreted as stationary epifauna, probably using iceberg strategy to be stabilized into the soft substrate.

Key words: Echinodermata, Diploporita, taxonomy, palaeoecology, Ordovician, Algeria, Stita.

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Introduction

Echinoderms represent a major component of Ordovician faunas, largely contributing to the Great Ordovician Biodiversification Event (e.g., Servais et al. 2008). Among them, diploporite and rhombiferan blastozoans, the so-called "cystoids", constitute emblematic clades of Ordovician benthic communities (Sprinkle and Guensburg 2004; Lefebvre et al. 2013). In mid to high latitude peri-Gondwanan regions of the southern hemisphere, aristocystitid diploporites were one of the dominant groups of Middle to Late Ordovician invertebrates, e.g., in Algeria (Termier and Termier 1950a), Burma (Bather 1906), China (Sun 1948), Czech Republic (Parsley 1990), France (Chauvel 1941, 1977, 1980; Chauvel and Nion 1969), Iran (Lefebvre et al. 2005), Morocco (Chauvel 1966, 1978; Álvaro et al. 2007), Portugal (Couto and Gutiérrez-Marco 1999), and Spain (Chauvel and Meléndez 1986; Gutiérrez-Marco and Baeza 1996; Gutiérrez-Marco and Aceñolaza 1999; Gutiérrez-Marco 2000; Gil Cid and García Rincón 2012).

Ordovician echinoderm faunas have been superficially investigated in Algeria. Termier and Termier (1950a) reported the presence of diploporite blastozoans in the Middle

Ordovician of northern Algeria (Great Kabylia). Since this pioneer but incomplete study, no further palaeontological investigation has been conducted on the Ordovician Algerian "cystoids". The aim of this study is to describe and revise taxonomically the poorly known aristocystitid species *Lepidocalix pulcher* Termier and Termier, 1950a, from the Middle Ordovician of northern Algeria. Its particular morphology could contribute to improve the discussion about the palaeoecology of the diploporites.

Institutional abbreviations.—MUA, Musée de l'Université d'Alger, Algeria.

Other abbreviations.—BB, basals; CO, circum-oral; COO, circum-orals; F, facetals; ILL, infralaterals; LL, laterals; OO, orals; PO, peri-oral; POO, peri-orals; RR, radials; UEH, Universal Elemental Homology.

Historical background

The presence of Palaeozoic strata in Great Kabylia was first acknowledged by Lambert (1939), based on the discovery of *Orthoceras* and *Tentaculites* in limestone beds previously assigned to the Infralias by Ficheur (1888).

On the northern edge of the Kabylian mountains, the occurrence of Ordovician echinoderms was first reported by Barbier et al. (1948), based on material collected in the "schistes X" (Darriwilian) at three distinct outcrops. The main locality is situated near the confluence of Wadi Stita and Wadi Sebaou, on the southern side of a hillock called the Zaouia. This outcrop yielded *Protocrinites* cf. *oviformis* Eichwald, 1840, large thecae of *Sphaeronites* sp., *Sinocystis* sp., and isolated plates of *Sinocystis* cf. *yunnanensis* (Reed 1917). The second fossiliferous site is located about 1500 m southeast of the right bank of Wadi Sebaou. The fauna is similar to that of the first locality, but with a higher abundance of *Sphaeronites* sp. The last outcrop (Akaoudj village) yielded small individuals of *Sphaeronites*. All Darriwilian echinoderm assemblages from Kabylia consist only of diploporites.

The presence of a younger (Katian) echinoderm fauna was also reported by Lambert et al. (1948) in calcareous and micaceous shale, on the northern flank of the Djurdjura (Fig. 1). This Late Ordovician echinoderm assemblage is composed exclusively of rhombiferans: *Heliocrinites rouvillei* von Koenen, 1886, *Corylocrinus* cf. *crassus* von Koenen, 1886, *Echinosphaerites* sp., and *Caryocystites* sp.

In the Darriwilian schists of the Zaouïa Formation (Fig. 1), the occurrence of two new diploporite "cystoids" characterized by several small and imbricate thecal plates was briefly mentioned by Termier and Termier (1948). The first one was described as an "amphorid". It shows an oral zone with four brachiole facets covered by ambulacral plates (Termier and Termier 1948). The second one was interpreted as an asteroblastid. It is characterized by a pentameric peri-

stome connected to ladder-shaped ambulacra (Termier and Termier 1948).

The whole Ordovician echinoderm fauna from Kabylia was reinvestigated and described in more detail by Termier and Termier (1950a). The two Darriwilian "cystoids" from Stita were named: *Lepidocalix pulchrum* (aristocystitid diploporite) and *Barbieria stitensis* (sphaeronitid diploporite). The associated echinoderm fauna from the same outcrop was also reported. It includes *Sphaeronites* sp., *Sinocystis* sp., and undescribed crinoids. The Katian "cystoid" fauna from the Djurdjura was also revised by Termier and Termier (1950a), who identified *Caryocrinites* cf. *elongatus* (Jaekel, 1899), *Caryocystites* sp., *Echinosphaerites* sp., *Heliocrinites rouvillei* von Koenen, 1886, and *Sphaeronites* sp.

Recently, Botquelen et al. (2006) briefly described crinoid columnals (*Squameocrinus* sp. and *Ristnacrinus* cf. *cirrifer* Le Menn in Chauvel and Le Menn, 1973) and several isolated rhombiferan thecal plates from younger deposits (Late Katian) at Oued Isser (on the edge of the Kabylian Massif).

Finally, an Ordovician echinoderm Lagerstätte (of ?latest Darriwilian to Sandbian age) was recently discovered in screes close to Ougarta village in western Algeria during geological field work performed for the Ceramines Agency, providing abundant specimens of the eocrinoid *Ascocystites* Barrande, 1887 (Makhlouf et al. 2010). Additional field work in the Bou M'Haoud Formation of the Ougarta Range (Foum Ezzeïdya, Kerzaz area, western Algeria) resulted in several fully articulated individuals of the eocrinoid *Ascocystites* Barrande, 1887. All specimens are preserved as delicate imprints in Upper Ordovician sandstone (Makhlouf et al. 2015). The same formation had previously delivered

System	Global series	Global stages	Unit of Great Kabylia
Ordovician	Upper	Hirnantian	
		Katian	Limestone of Djurdjuran
		Sandbian	
	Middle	Darriwilian	Schists of Zaouïa
			Tuffs of Akaoudj
		Dapingian	
	Lower	Floian	
		Tremadocian	Schists of Thadalout

Fig. 1. Lithostratigraphic units defined in Great Kabylia (after Termier and Termier 1950a; Baudelot and Géry 1979).

(Ghienne et al. 2007) indeterminate echinoderm remains in several sections: Foum Ezzeïdya, Sebkhet el Melah, Djebel Bou Kbaissat and Kheneg Tlaïa.

Geological setting

In Tellian areas, the extent of Palaeozoic outcrops is restricted to a few occurrences in a limited number of regions: Ghar-Rouban Mountains, Tiffrit, Traras, Chenoua, Great and Lesser Kabylia.

Great Kabylia belongs to the Maghrebides, and is a part of the Alpine peri-Mediterranean orogeny (Durand-Delga 1969). This chain is composed of orogenic segments straddling over 2000 km, from the Strait of Gibraltar to the north of Calabria (Italy), and comprising the Moroccan Rif, the Atlas coastline of Algeria (Kabylia and Tell), the Atlas of Tunisia, Sicily, and Calabria (Aubouin 1977; Durand-Delga and Fontboté 1980). It probably results from the convergence and collision of an element of the southern European margin with the northern African margin of the Maghreb Tethys basin (Wildi 1983).

The two historical Darriwilian outcrops yielding echinoderm remains are located in Great Kabylia: Zaouïa of Stita and Akaoudj (Fig. 2). These two localities belong to the Aïssa Mimoun Massif, and they are about 29 km away from the Katian outcrops of northern Djurdjura.

The original type locality of *Lepidocalix* is located in the Zaouïa of Stita (Fig. 2) in the north-western part of Great Kabylia, at the confluence of Wadi Stita and Wadi Sebaou at about 5 km northeast of Tizi-Ouzou, in the municipality of Makouda.

In addition to the aristocystitid *Lepidocalix pulcher* Termier and Termier, 1950a, this locality yielded a diverse associated fauna comprising brachiopods (*Strophomena barbieri* Termier and Termier, 1950a; *Leptaena* cf. *trigonalis* Schmidt, 1908, and *Strophomena* (*Actinomena*) *orta* Öpik, 1930), graptolites (*Inocaulis*? *gigas* Termier and Termier, 1950a; *Airograptus*? *betieri* Termier and Termier, 1950a, *Thallograptus barbieri* Termier and Termier, 1950a, and *Dendrograptus* sp.), and trilobites (*Pharostoma pulchra* [Barrande, 1846], and *Colpocoryphe arago* [Rouault, 1849]). The Zaouïa of Stita assemblage is preserved in slightly metamorphosed green or grey micaceous mudstone with many intercalated tuff beds similar to those of Akaoudj. The associated acritarch fauna (Baudelot and Géry 1979) confirms the Darriwilian age proposed by Termier and Termier (1950a) based on the macrofauna.

Material and methods

All specimens of *Lepidocalix* studied here were originally briefly described and illustrated (as rough line drawings) by Termier and Termier (1950a). None of them is complete, and all lack ambulacral appendages and are preserved as
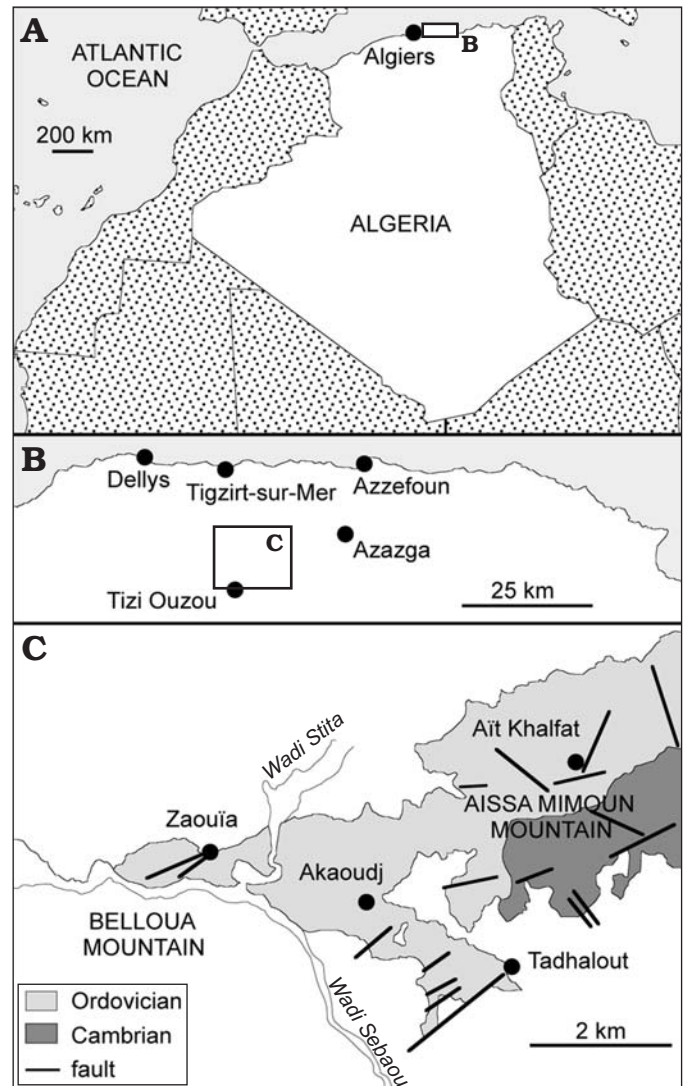

Fig. 2. General map of Algeria (**A**) and northern Algeria (**B**) showing location of the fossiliferous sites (solid circles). **C**. Geological map of Aissa Mimoun Mountain (Great Kabylia) and location of the studied section (Zaouïa of Stita).

partial thecae, which is a frequent case in organisms with multi-element skeletons (Brett et al. 1997). Where part and counterpart moulds are available, both external and internal surface of the same part of the theca can be studied (MUA.1024020 and MUA.1023001). The rest of the material only reveals external surface, probably crushed before complete burial. The tectonic distortion of the study material prevented any attempt at providing a detailed reconstruction of all aspects of its original morphology.

The six examined specimens are deposited in the collections of the Museum of Algiers University. Their preservation as internal or external empty moulds made it necessary to prepare latex casts, whitened with ammonium chloride. These casts were observed, drawn and photographed using a Zeiss SteREO Discovery V8 stereomicroscope equipped with a camera lucida and a Zeiss Axio Cam MRc5 digital camera.
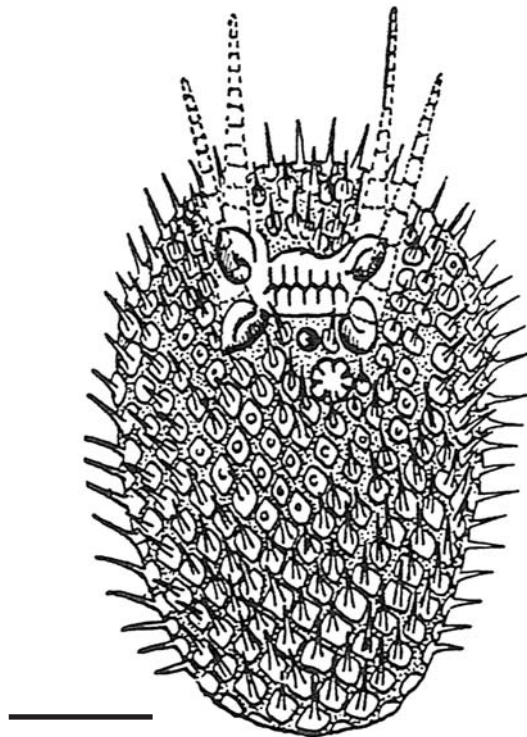
Fig. 3. Original reconstruction of the diploporite blastozoan *Lepidocalix pulcher* Termier and Termier, 1950a (see Termier and Termier 1959; Kesling 1968). Scale bar 10 mm.

Terminology.—Until recently, the very high morphological disparity displayed by blastozoans ("cystoids") made it particularly difficult to identify thecal plate homologies, and thus to define a common terminology for all classes. The system of plate designation proposed by Jaekel (1899) for glyptocystitoid rhombiferans was further elaborated by Regnéll (1945), Kesling (1963, 1968), and Paul (1967). In this model, the theca can be subdivided into five circlets of plates: BB, ILL, LL, RR, and OO. In glyptocystitoids, the seven oral plates are consistently located in interradial position: in the AB (O4), BC (O5), CD (O1, O6, and O7), DE (O2), and AE (O3) interrays. Thecal plate homologies in diploporite cystoids were first investigated by Paul (1973), who proposed two distinct terminologies for skeletal elements framing the peristome: circum-oral plates in sphaeronitids, and peri-oral plates in holocystitids (Paul and Bockelie 1983). Paul (1973) did not use the same plate designation as in glyptocystitoids, so as to avoid any implication in terms of homologies: for example, the radial position of several COO in sphaeronitids makes it difficult to consider them as equivalent to the interradial OO of glyptocystitoids (Paul 2017).

Recently, the terminology originally defined for the plates framing the peristome in glyptocystitoids was applied to blastoids, coronates, diploporites, eocrinoids, and paracrinoids (Sumrall 2008, 2010, 2015; Sumrall and Waters 2012; Kammer et al. 2013). The generalization of this model, coined UEH by Sumrall (2008), represents a major advance for blastozoan phylogeny. However, the very distinctive plate patterns displayed by some diploporites question the universality

of this model (Paul 2017). In holocystitids and protocrinitids, the plate pattern of the oral area is compatible with the UEH (Sumrall 2008, 2010, 2015; Sheffield and Sumrall 2015): all skeletal elements framing the peristome are in interradial position, and the possibility that POO are equivalent to OO cannot be ruled out. In sphaeronitids, only two mouth frame elements are in interradial position (CO6 and CO7, in the CD interray) and can be tentatively compared with topologically equivalent plates in holocystitids (PO1 and F1) and/or other blastozoans (O6 and O7). The other elements forming the mouth frame in sphaeronitids are in radial position (CO1–5) and possibly correspond to enlarged facetals by comparison with other diploporites (Paul 1973, 2017; Paul and Bockelie 1983; but see Sumrall 2015 for a different interpretation).

The identification of the skeletal elements forming the mouth frame in aristocystitid diploporites has been so far largely neglected in all systematic descriptions (e.g., Chauvel 1966, 1977, 1978, 1980; Parsley 1990; Gutiérrez-Marco and Aceñolaza 1999; Gutiérrez-Marco 2000; Gil Cid and Garcia Rincon 2012), as well as in all recent surveys dealing with plate homology in blastozoans (e.g., Paul 1973; Sumrall 2008, 2010, 2015; Sumrall and Waters 2012; Kammer et al. 2013). This situation probably results from the limited number of specimens showing well-preserved oral areas. The peristome of aristocystitids is delimited by a variable number of plates: four to six elements are in interradial position and represent putative homologues of POO in holocystitids and/or OO in other blastozoans; two (*Aristocystites*), three (*Triamara*), four (e.g., *Calix*, *Lepidocalix*), or five (*Oretanocalix*) other plates are in radial position. These radial mouth frame elements are very likely equivalent to COO in sphaeronitids and have no equivalent in other blastozoans.

Consequently, the UEH terminology is not followed herein. This model does not provide any clues for the identification of radial mouth frame elements in both aristocystitids and sphaeronitids. In *Lepidocalix*, only four plates involved in the peristomial margin could be putatively compared with topologically equivalent elements in other blastozoans (O3 and O4 in the BE interray, O1 and O6 in the CD interray). On the other hand, the plate designation proposed by Paul (1971) for mouth frame elements in diploporite cystoids makes it possible to identify all plates in *Lepidocalix*, and to compare its plate pattern with those of both holocystitids and sphaeronitids. Discussion about putative homologies of interradial mouth frame elements in diploporites and other blastozoans is beyond the scope of this paper, as it would require the detailed reexamination of the oral surfaces of all (most) aristocystitid genera.

Systematic palaeontology

Subphylum Blastozoa Sprinkle, 1973

Class Diploporita Müller, 1854, Paul (1972)
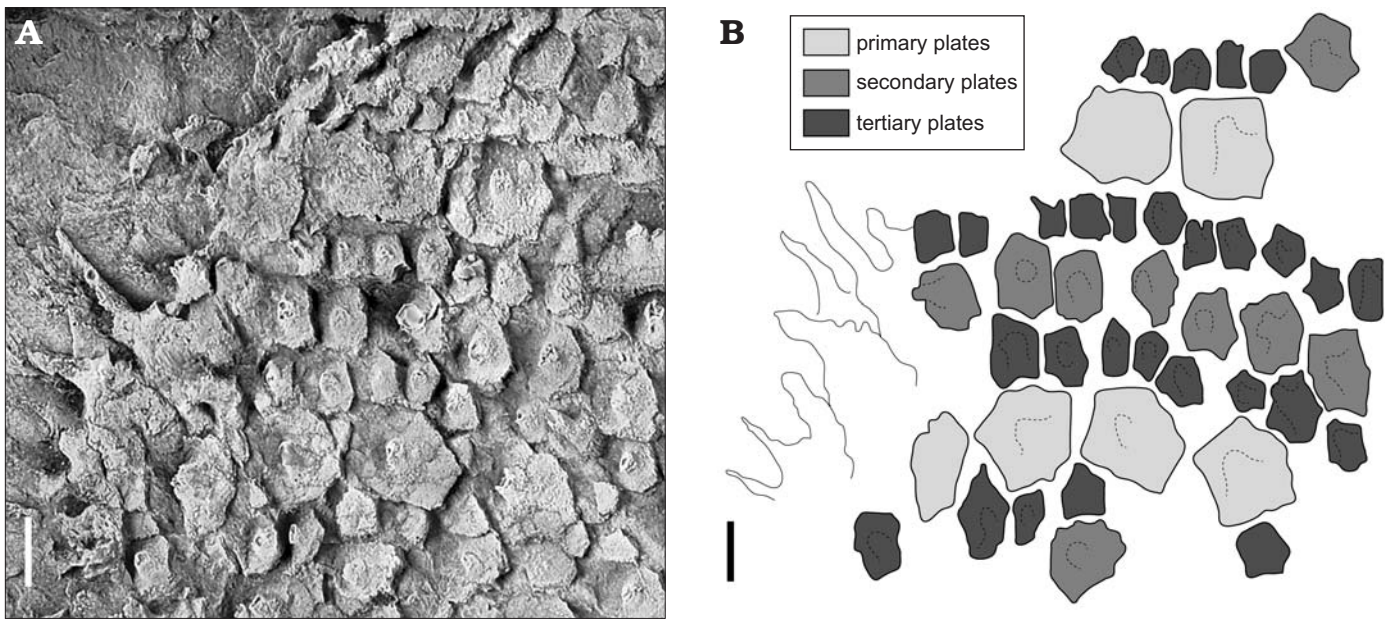
Superfamily Aristocystitoida Neumayr, 1889

Fig. 4. Diploporite blastozoan *Lepidocalix pulcher* Termier and Termier, 1950a (MUA. 1023001); Middle Ordovician, Stita, Algeria. **A**. Photograph of latex cast of external mould showing spines, tubercles, and the appearance of imbricate plates. **B**. Camera lucida drawing, note three generations of plates. Scale bars 2 mm.

Family Aristocystitidae Neumayr, 1889
Subfamily Calicinae Termier and Termier, 1950b

Diagnosis (translated from Chauvel 1966).—Aristocystitids with an elongate to pyrifom theca, composed of numerous plates regularly (juvenile stages) to irregularly organised. Plate surface flattened to convex and bearing central umbo to well-developed spine. Roundish to elliptical peripores including one large diplopore, sometimes covered by a tubercle. Elongate peristome central to a four-fold ambulacral system.

Remarks.—The subfamily Calixinae (sic!) was erected by Chauvel (1966) after the revision of the family Calicidae Termier and Termier, 1950b to emphasize the singularity of this taxonomic group. Kesling (1968) did not acknowledge the different subfamilies (Aristocystitinae, Calicinae, and Hippocystinae) identified by Chauvel (1966) within the family Aristocystitidae. Until a detailed phylogenetic analysis of aristocystitids is performed, Chauvel's (1966) systematic scheme is followed here, and his original diagnosis of the subfamily Calicinae is here simply translated from French to English. The subfamily Calicinae differs from the two other ones by the shape of the diplopores, the presence of a strong ornamentation, the small size of thecal plates, and the ambulacral pattern.

Genus *Lepidocalix* Termier and Termier, 1950a

Type species: Lepidocalix pulchrum Termier and Termier, 1950a, monotypic, see below.

Diagnosis.—As for type species by monotypy.

Remarks.—The original description of the species did not contain a diagnosis (see Termier and Termier 1950a). The diagnosis proposed here has been emended from the only previously published one by Kesling (1968; Fig. 3).

Lepidocalix pulcher Termier and Termier, 1950a

Figs. 4–6.

1950 *Lepidocalix pulchrum* sp. nov.; Termier and Termier 1950a: 26, pl. 8: 2, 3.
1959 *Lepidocalix pulchrum* Termier H. & G., 1950; Termier and Termier 1959: 89, 498.
1968 ?*Lepidocalix pulchrus* [sic] Termier and Termier, 1950a; Kesling 1968: 254, 143.
2011 *Calix pulchra* (Termier and Termier, 1950a); Gutiérrez-Marco and Colmenar 2011: 190.

Type material: Lectotype (MUA. 1024020), a flattened theca showing the oral zone. Paralectotypes (MUA. 1023001, MUA. 1023002, MUA. 1024016, MUA. 1024021 and MUA. 1024022), by fragmentary samples.

Type locality: Zaouïa of Stita, Great Kabylia, northern Algeria.

Type horizon: Darriwilian, Middle Ordovician.

Emended diagnosis.—Calicinae with an elongate theca composed of abundant, thin, and small thecal plates organised in circlets. Primary plates bear up to three dipores, while secondary and tertiary plates, one tubercular diplopore. Relatively small and elongate peristome connected to two main ambulacral rays subdivided once laterally. Ambulacral rays and peristome covered by two series of polygonal cover plates. Periproct restricted to an anal pyramid composed of triangular plates. Slit-like hydropore located between the peristome and the periproct in the CD interray.

Description.—The theca is composed of small, numerous (hundreds), adjacent plates of various sizes, revealing three generations of plates (Fig. 4). The largest preserved

theca reaches 62 mm in diameter (MUA.1023002). Primary plates are pentagonal in shape, sometimes hexagonal with rounded corners. Each primary plate carries one central spine and sometimes one or two tubercles. Secondary and tertiary plates are smaller, hexagonal to irregularly polygonal. They sometimes bear one small tubercle (Fig. 5A$_2$). In larger specimens, primary plates are up to 3 mm wide and 4.5 mm long, while secondary and tertiary elements are up to 2 mm in diameter (MUA. 1023001). All plates are thin at their edges, less than 0.25 mm in thickness. Plates appear to be aligned to form continuous circlets reflecting three generations of circlets. Spines are narrow and elongated (up to 5 mm long). They have a large base, up to the width of the plate, and taper distally, becoming elliptical (no articulation of spines was observed). They are adorally orientated with their base located at the aboral side of the plate. Perpendicular canals can be observed within abraded tubercles and spines. Each secondary and tertiary plate bears one tubercle thinly covering one superficial diplopore. The pattern in the primary plates is more complex. Their spines shelter one internal diplopore, while their tubercles can cover one haplopore or two perpendicular but sinuous canals possibly connected to form a diplopore. Externally the pores can only be seen where the spines have been damaged. Specimens MUA.1024016 and MUA.1023002 confirm the presence of fine spiny ornament on the facetal plates around the ambulacral facets (Fig. 5B, C). The latter reach about 3 × 3 mm, are slightly concave and appear to have supported a single, robust ambulacral appendage, none of which is preserved.

The dipores consist of narrow paired canals about 0.2 mm in diameter (MUA.1023001B). Internally some openings increase in diameter as they reach the internal surface. In the lectotype, pores open externally in an oval tubercle (width 0.65–0.7 mm; length 0.8–0.9 mm) with individual pores about 0.35 mm in diameter. The tubercles apparently represent damaged spines. Specimen MUA.1024016 shows lateral views of some damaged spines that appear to have canals within them (Fig. 5B$_1$). The variability of the pores apparently depends on where the original spines were damaged (MUA.1024022; Fig. 5D).

The oral surface is slightly flattened at the top of the theca (MUA.1023002). Peristome is a wide, transversally elongated slit (5 mm wide), with two short ambulacra diverging from each extremity and ending in large obovate ambulacral facets (Fig. 6A). It is approximately 20 mm wide by 13 mm in the presumed anterior-posterior direction (MUA. 1024020A). Peristome is framed by eight plates (Fig. 6A): four circum-orals in radial position (CO1, CO2,

CO4, and CO5) and four peri-orals in interradial position (PO1, PO3, PO4, and PO6). The A ambulacrum is absent, thus leading to a four-fold ambulacral system. Ambulacral facets are deep and large (0.75 mm) recumbent on larger oral plates. Peristome is covered by two series of triangular to polygonal plates, and ambulacra, by one series of polygonal plates. The internal surface shows no trace of a central oral opening (mouth), while the oral plates show many dipores with no clear corresponding openings on the external surface (MUA. 1024020B; Fig. 6B).
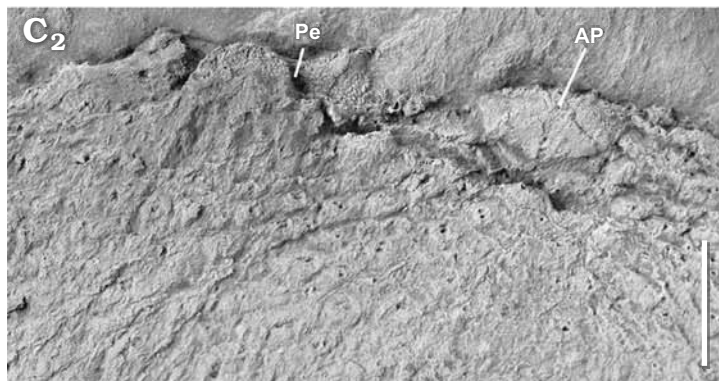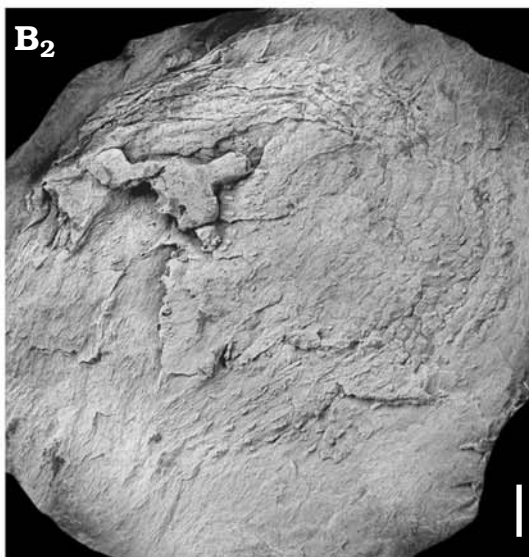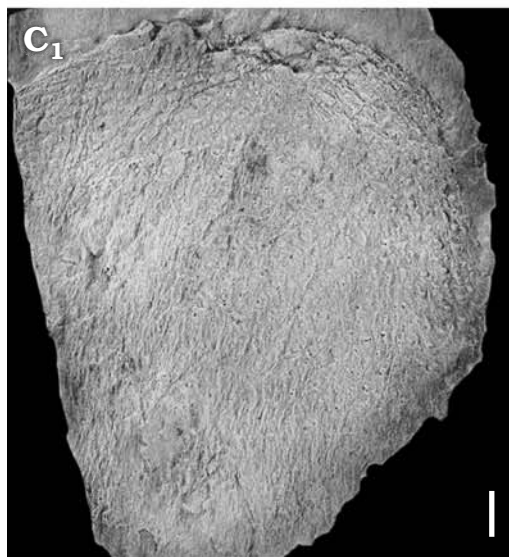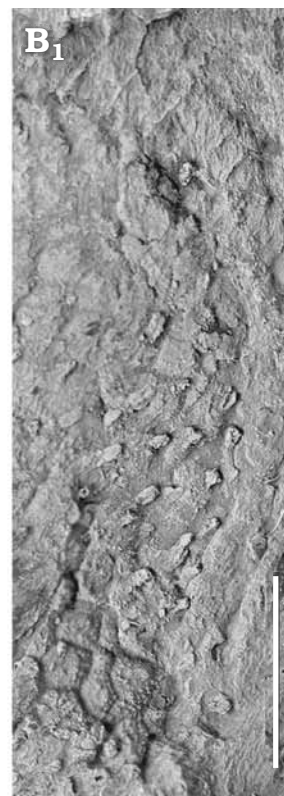
The periproct corresponds to a roundish anal pyramid composed of 7 smooth triangular plates (MUA.1023002A). It is about 6 × 3 mm, despite a slight crushing. Hydropore is a slit-like fold located in the CD interray across the PO1–PO6 suture. The gonopore and the aboral region are unknown.

Remarks.—The masculine of the Latin word for beautiful is *pulcher* not *pulchrus. Calix* is masculine, so we assume *Lepidocalix* will be too. Thus the correct form would be *Lepidocalix pulcher* Termier and Temier, 1950a. The subfamily Calicinae is characterized by a four-fold ambulacral system, as shown in *Calix sedgwicki* Rouault, 1851; *Calix inornatus* (Meléndez, 1958); *Glaphocystis globulus* Chauvel, 1966; *Sinocystis loczyi* Reed, 1917; *Sinocystis gigas* (Termier and Termier, 1950a), and *Phlyctocystis* sp. (Chauvel, 1978). The ambulacral facets of *Lepidocalix pulcher* appear to have given rise to a single appendage or brachiole each. In contrast, in *Calix sedgwicki* Rouault, 1851, each of the four ambulacral facets bears four brachioles. The presence of this four-fold ambulacral pattern combined with the possession of the typical thecal plating of Calicinae, both support the assignment of *Lepidocalix* to this subfamily.

The plates of *Lepidocalix* are very thin (0.25–0.3 mm thick), whereas most aristocystitids have plates over 1 mm thick (e.g., *Calix*) and many over 2–3 mm (e.g., *Pachycalix*). Their plates are very small and only have a maximum of 3 diplopores per plate, while most aristocystitids have several tens (20–30 at least) of diplopores in their largest plates. The plates bear very prominent spines over the diplopores. These spines reach 3 times as long as the plates are wide. *Sinocystis* has short tubercles over individual diplopores, but these are a fraction of one mm high and the plates are covered with the tubercles. "Spiny" plates in *Calix* are much thicker, the plates bear numerous diplopores often distributed all over the "spines".

In general, these aristocystitids are characterized by a more elongate, ellipsoidal theca, composed of generational circlets of plates showing an ornamentation strongly linked to the development of the respiratory structures (Chauvel

Fig. 5. Photographs of latex casts of the diploporite blastozoan *Lepidocalix pulcher* Termier and Termier, 1950a; Middle Ordovician, Stita, Algeria. →
A. MUA. 1023001; general aspect of the theca, in lateral view (A$_1$); enlargement of external surface (A$_2$, turned 90° counter clock-wise), showing the central tubercles on the plates; enlargement of inner surface (A$_3$), showing the distribution of the diplopores and apparent imbrication of plates. **B**. MUA. 1024016; summit view of the theca (B$_2$), showing circlets of tessellate thecal plates; enlargement of the summit (B$_3$, turned 90° clockwise), composed of four ambulacral rays recumbent on ornamented facetal plates; enlargement of the right thecal periphery (B$_1$), showing tessellate plates ornamented with tubercles and long spines. **C**. MUA. 1023002; general outline of the theca (C$_1$); enlargement of the top of C$_1$ (C$_2$), showing the organisation of the peristome (Pe) and the periproct (AP). **D**. MUA. 1024022, showing some abraded spines revealing the diplopores. Scale bars 5 mm.
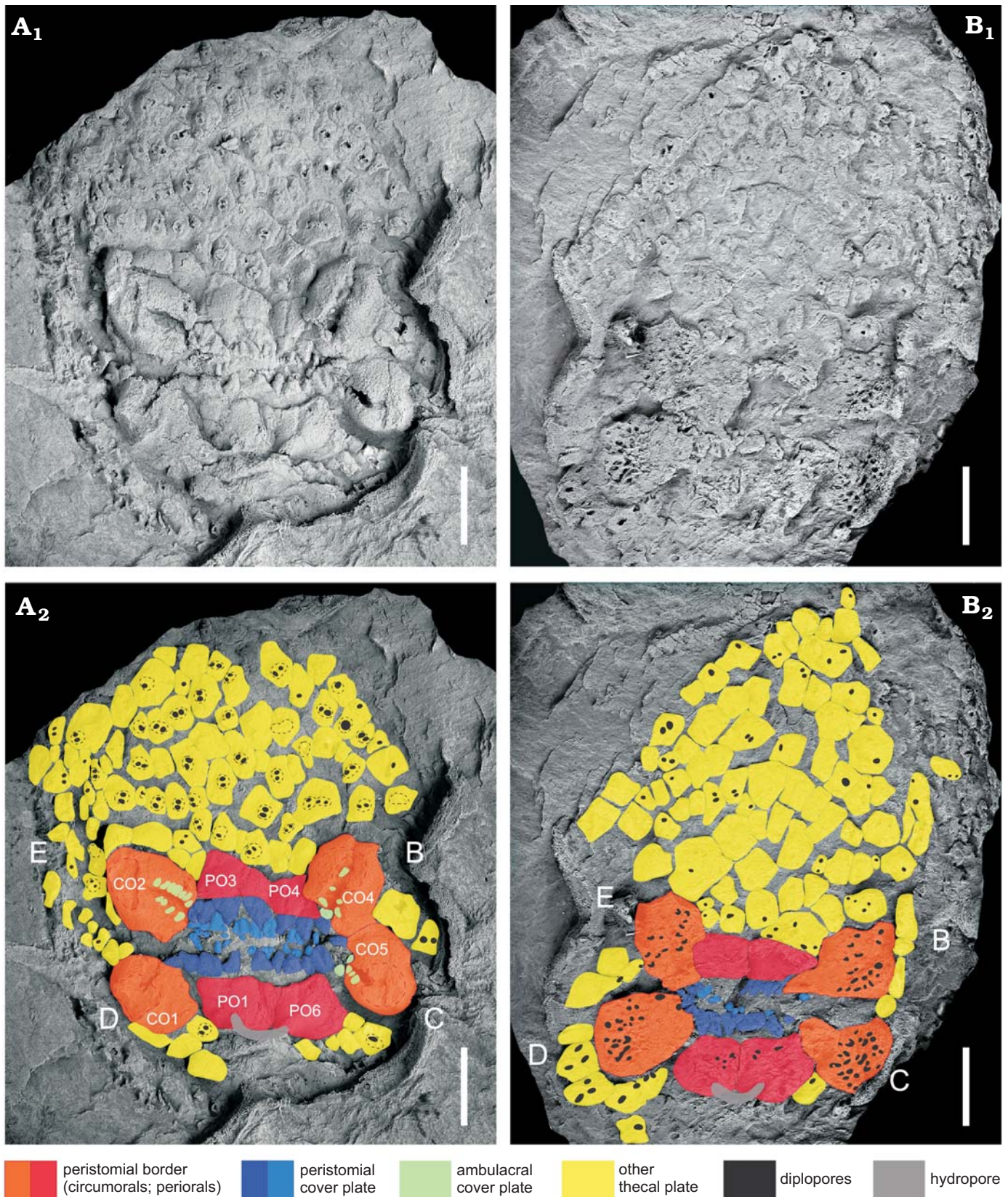
Fig. 6. Oral surface of the diploporite blastozoan *Lepidocalix pulcher* Termier and Termier, 1950a (MUA. 1024020); Middle Ordovician, Stita, Algeria.
A. Four peri-orals (PO1, PO3, PO4, and PO6) between four circum-orals (CO1, CO2, CO4, and CO5), peristome partially covered by small subtriangular oral cover plates biseries, diplopore-bearing polygonal thecal plates immediately surrounding the peristome, hydropore over PO1 and PO6; in external view. **B**. Surface showing numerous diplopores. Photographs (A₁, B₁), coloured interpretations (A₂, B₂) of both surfaces illustrating names using circumorals and periorals (Paul 1973, 2017); in internal view. B–E ambulacral designations in Carpenter's system. Scale bars 5 mm.
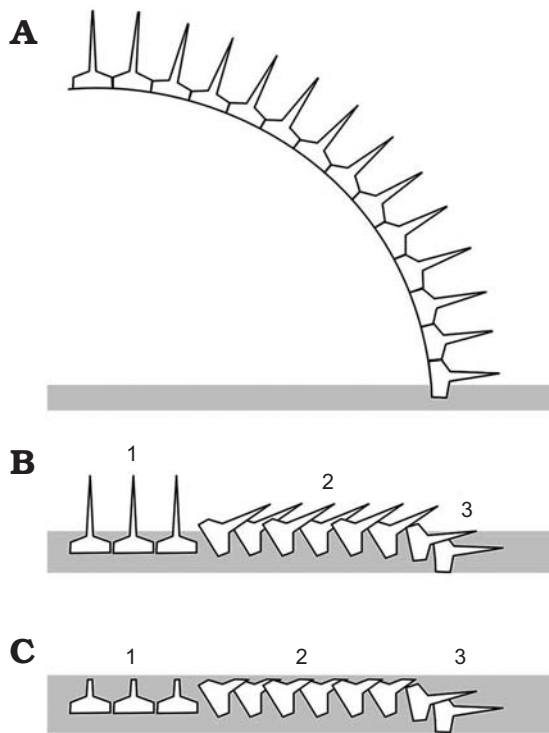
Fig. 7. Interpretation of taphonomy of the diploporite blastozoan *Lepidocalix pulcher*. **A**. Original disposition of partial theca still articulated. **B**. Positions of isolated plates after decay of ligaments and possible accumulation of a little more sediment (grey). Three areas can be distinguished. 1, areas where the spines were directed upwards in which the plate orientation has not changed significantly; 2, areas where the plates have rotated slightly so the spines rest on adjacent plates; 3, peripheral areas where the plates have again not rotated significantly, but the spines are buried in the sediment. **C**. Final stage of preservation in which parts of the plates not buried in sediment have been eroded, leaving plates in areas 1 and 2 lacking complete spines, those in area 2 apparently imbricate and spines only preserved in area 3.

1966, 1980; Chauvel and Meléndez 1978; Kesling 1968). The general thecal shape of *Lepidocalix* is difficult to reconstruct, because of its preservation. The larger specimen (MUA. 1023002) shows a circular outline with a slightly flattened oral region. The specific plating organised in circlets leads us to suppose an original cylindrical shape of the theca (Paul 1971; Frest et al. 2011). It could therefore be similar in thecal shape and plating to *Calix* and *Phlyctocystis*, both possessing a conical theca, composed of numerous circlets of three generations of plates (Chauvel 1978). Thecal plating in circlets is a diagnostic characteristic of the subfamily (Chauvel 1966). However, it is more strongly expressed in all *Calix* species, and only in the aboral regions of the species of *Sinocystis* and *Glaphocystis* (Chauvel 1966). Ornamentation as spines and/or tubercles is also known in several species of *Calix*. However, these ornamentation features are usually restricted to the primary plates in the aboral part of the theca, as in *Calix sedgwicki* and *Calix segaudi* Termier and Termier, 1950b. In contrast, the outer surface of *Calix inornatus* is smooth, and without tubercles. All specimens of *Lepidocalix* studied here show spines and

tubercles distributed all over the theca. A final major singularity of *Lepidocalix* among its subfamily is in grade, based on the presence of an extremely reduced number of dipores per thecal plate.

Termier and Termier (1950a) described imbricate thecal plating in *Lepidocalix*. However, new series of latex casts of their original material show tessellate sutures between primary and secondary/tertiary plates and no hollow on the external surface of the plates suggesting any plate overlapping (Fig. 5A). When buried, the spines caused the plates near the edge of the specimens to rotate slightly producing the apparently imbricate appearance of some plates, because these spines were initially at an oblique angle to the sediment surface (Fig. 7). In the centre of the specimen, plates would not have rotated but simply been forced down onto the sediment surface by compaction. Nevertheless, the spines were not completely buried, so that in the centre of specimens they are truncated and often reveal the pore canals inside (similar hypothesis has been proposed for sphaeronitid diploporites; Bockelie 1984). So, the plates are usually still articulated and do not show any apparent imbrication. This appearance is considered here as a preservational artefact, due to the crushing of the theca and the subsequent slight rotation of the spiny plates. Therefore, we reject the hypothesis of imbricate plating in *Lepidocalix*.

Stratigrapic and geographic range.—Type locality and horizon only.

Discussion

Respiratory structures.—Some thecal plates of *Lepidocalix* clearly show the presence of diplopores on the internal surface, but no sign of them on the external surface. Indeed, external pores are only seen, where the spines have been damaged. This suggests that the diplopores of *Lepidocalix* were very likely sealed externally by permanent periporal roof forming the spine, like many representatives of Aristocystitidae but less developed (Bockelie 1984; Parsley 1990). Such covered diplopores are not uncommon in *Aristocystites* and *Sinocystis* and probably other aristocystitid genera. Parsley (1990) illustrated covered diplopores in *Aristocystites bohemicus* Barrande, 1887, and no trace of diplopores can be observed externally in *Aristocystites metroi* Parsley and Prokop in Parsley, 1990. This would reduce their respiratory capacity by up to about 50% (Paul 1976), by reducing their effective exchange surface area while maintaining their role in the respiratory exchange (Paul 1972). Sealed diplopores of *Lepidocalix* are within the range of variation seen in other species from the family Aristocystitidae. Bather (1919) illustrated some diplopores of *Sinocystis* which were at the tips of calcite tubercles and similar to those of *Lepidocalix*. Bockelie (1984) suggested that the diplopore calcitic sealing could have protected from predation of soft tissue or prevented toxic gas poisoning.

However, the latter is unlikely: if the diplopores could still exchange oxygen, they could still exchange other (toxic) gases. The presence of numerous long spines might favour the first hypothesis.

The number of dipores increases with the size of plates. There is evidence that the number of dipores could increase during plate growth. The appearance of new diplopores at the plate sutures could occur without resorption of the plate epistereom in *Lepidocalix* (Paul 1971, 1973; Bockelie 1984; Parsley 1990), where, nascent formation of dipores has not been observed.

Mode of life.—Aristocystitids appear to have developed three strategies to stabilize the theca on the substrate. *Aristocystites* Barrande, 1887, has an obvious attachment area developed aborally allowing its settlement on to hard substrates at least early in ontogeny. *Aristocystites* has a recumbent mode of life (Parsley 1990). It often has very thick plates aborally as in *Magrebocystis* Chauvel, 1966, which was proposed to live either attached to shell fragments or resting upward into a loose sediment, stabilized by their thick base (Chauvel 1978). In contrast, *Calix* Rouault, 1851, often has an aboral, stem-like extension to the theca (Chauvel 1966; Gutierrez-Marco and Colmenar 2011). With *Phlyctocystis*, it has an erect mode of life with aboral structure of attachment (Gil Cid and Domínguez-Alonso 2001). We have seen no evidence of any attachment structures; although the thinness of the thecal plates would conflict with thickened basal plates. Large preserved thecal fragments encompass two-thirds of the reconstructed thecal length. The specimens of *Lepidocalix* are preserved in a slightly metamorphic mudstone with few complete wide strophomenid shells, in addition to graptolites and leaf-shaped bryozoans. The specimens of *Lepidocalix* might have lived on a soft substrate among a low-level suspension feeder community, as stationary epifauna possibly with the basal theca partly implanted into the soft sediment, using either an iceberg strategy or as a shallow sediment sticker or rester (Thayer 1975; Chauvel 1941, 1966, 1978; Bottjer and Ausich 1986; Brett 1991; Gil Cid and Domínguez-Alonso 2001; Dornbos et al. 2005).

Conclusion

Lepidocalix pulcher Termier and Termier, 1950a is characterized by a large theca organised in circlets of plates, few diplopores per plate, and a four-fold ambulacral system. The genus is now assigned to the subfamily Calicinae Termier and Termier, 1950b. Our description of the species enables us to propose a diagnosis emended from Kesling (1968). The major singularity is the presence of a reduced number of dipores per thecal plate, with frequently one dipore per plate. Larger specimens show three generations of thecal plates; the primary plates bearing up to three dipores each. Diplopore addition during growth could therefore have oc-

curred at the suture of plates without resorption (Paul 1971, 1973; Bockelie 1984; Parsley 1990). The dipores are covered, as in many representatives of the Aristocystitidae, which would result in a reduction of the respiratory capacity, by decreasing the exchange surface area (Paul 1972). The thecal plates are ornamented by tubercles and spines; the latter hosting the diplopores. Both ornaments constitute the extension of plate epistereom. They might favour the hypothesis of protection from predation on soft tissue (Bockelie 1984). During fossilization, some spine-bearing plates rotated, thus producing their apparently imbricate appearance. The imbricate thecal plating in *Lepidocalix* described by Termier and Termier (1950a), is therefore considered here as preservational artefact. All specimens of *Lepidocalix* are preserved in a slightly metamorphic mudstone. Despite the absence of preserved aboral region, we suggest that *Lepidocalix* probably lived on the substrate as stationary epifauna (Bottjer and Ausich 1986; Brett 1991).

Acknowledgements

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