

Oldest mickwitziid brachiopod from the Terreneuvian of southern France

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Kerberellus marcouensis Devaere, Holmer, and Clausen gen. et sp. nov., originally described as *Dictyonina?* sp., from the Terreneuvian of northern Montagne Noire (France) is re-interpreted as the oldest relative to or member of mickwitziid-like stem-group brachiopods. We extracted 170 partial to complete phosphatic internal moulds of two types of adult and one type of juvenile disarticulated valves, rarely externally coated with phosphates, from the calcareous *Heraultia* Member of the Marcou Formation. They correspond to microbially infested, ventribiconvex, inequivalved, bivalved shells. The ventral interarea is bisected by a triangular sinus. The shell, most probably dominantly organic in origin, is orthogonally pierced throughout its entire thickness by radially-aligned, smooth-walled, cylindrical to hour-glass shaped canals except for the sub-apical planar field (interarea). The through-going canals of *K. marcouensis* are compared with brachiopods endopunctae and with canals of mickwitziid brachiopods. The absence of striations on *K. marcouensis* canal walls, typical of mickwitziids, implies that (i) the tubes could have been depleted of setae or; (ii) traces of the microvilli were not preserved on the tube wall (taphonomic bias) or, (iii) the tubes could have been associated with an outer epithelial follicle.

Key words: Brachiopoda, Mickwitziidae, shell canals, Cambrian, Terreneuvian, West Gondwana, France.

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Introduction

The paterinate brachiopods *Aldanotreta* Pelman, 1977 and *Cryptotreta* Pelman, 1977 from the early Tommotian of Siberia have for a long time represented the earliest stratigraphical record of the phylum (Laurie 2000; Ushatinskaya 2008). These records were only recently challenged by new chemostratigraphical re-interpretation of Mongolian records of the very problematic, but superficially brachiopod-like *Khasagtina* Ushatinskaya, 1987 as Nemakit-Daldynian in age (Kouchinsky et al. 2010; Maloof et al. 2010; see also Popov and Williams 2000), but there are no other well-established Terreneuvian records of brachiopod-like forms; the first records of undoubted linguliform and rhynchonelliform brachiopods are from the Atdabanian (Holmer and Popov 1996; Popov et al. 1996; Ushatinskaya 2008).

The brachiopods from the lower Cambrian *Heraultia* Limestone were first monographically described by Kerber

(1988) and include two supposed paterinates *Paterina* sp. and *Dictyonina?* sp. New abundant material of the latter species—here described as *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov.—clearly shows that it does not share any characters with the paterinate brachiopods, but the pustulose ornamentation and punctate shell structure indicate affinity with the mickwitziids, which have been referred to the stem of the Brachiopoda (e.g., Holmer et al. 2002; Skovsted and Holmer 2003; Balthasar 2004; Holmer and Popov 2007).

The newly established Tommotian age (Cambrian Stage 2) of the upper *Heraultia* Limestone indicates that *K. marcouensis* is one of the oldest members of the phylum and it represents the oldest record of the mickwitziids, which are otherwise known from the Atdabanian–Toyonian interval (Holmer and Popov 2007).

Institutional abbreviations.—USTL, palaeontological collections of the University Lille 1, Villeneuve d'Ascq, France.

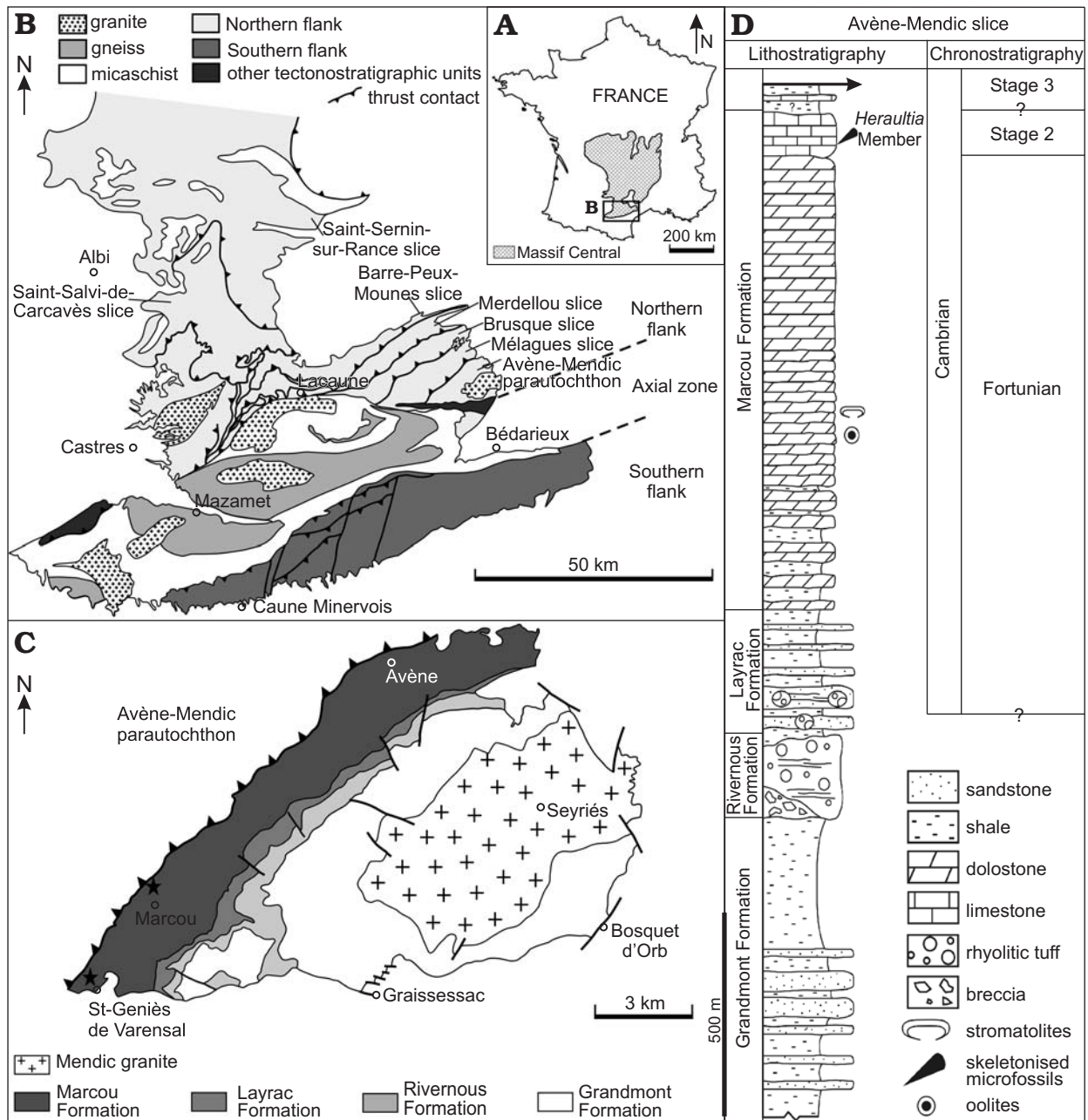


Fig. 1. Geological features of the Montagne Noire (modified from Clausen and Álvaro 2007; Devaere et al. 2013; and Álvaro et al. 2014). **A.** Location of the Massif Central and the Montagne Noire in France. **B.** Structural sketch of the Montagne Noire. **C.** Geological sketch of the Avène-Mendic parautochthon with location of the sections (asterisks) yielding *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. **D.** Litho- and chronostratigraphic setting of the Avène-Mendic Unit (after Devaere et al. 2013), the section is interrupted by a thrust contact with the Mélagues slice (symbolized by the arrow in the upper part of the log).

Geological setting

The Montagne Noire is the southernmost extremity of the Massif Central (Fig. 1A). This Variscan massif is surrounded by uppermost Carboniferous and other later post-orogenic sediments. The Montagne Noire is subdivided into three main structural domains (Bergeron 1887; Gèze 1949; Fig. 1B): (i) a metamorphic Axial Zone (Demange 1998), bordered by (ii) a southern flank, including lower Cambrian to Carboniferous rocks, and (iii) a northern flank, involving low-

er Cambrian to Silurian strata arranged in imbricate thrust slices (Guérangé-Lozes and Burg 1990). Five major tectonostratigraphic units compose the eastern part of the northern flank (called Lacaune Mountains), from SE to NW: the Avène-Mendic parautochthon (where the outcrops yielding *Kerberellus* are located; Fig. 1C) and the Mélagues, Brusque, Merdellou, and Barre-Peux-Mounes slices (Fig. 1B).

Recently, Álvaro et al. (2014) made a complete revision of the lithostratigraphic units and volcanic complexes of northern Montagne Noire. The succession of the Avène-Mendic parautochthon

tochthon consists of a volcanosedimentary complex (Fig. 1D) followed by a progressive onset of carbonate productivity named the Marcou Formation by Álvaro et al. (2014). Three distinct members can be recognised in this carbonate-dominated succession: (i) shale/dolostone alternations, (ii) a dolomitic masse, (iii) thin- to medium-bedded bioclastic limestone rich in phosphatic hardgrounds, hardground-derived clasts and phosphatised skeletons called the *Heraultia* Limestone Member. The cyclic deposition of the *Heraultia* Limestone took place in a stable inner shelf to an unstable slope-to-basin seafloor (Clausen and Álvaro 2007; Álvaro and Clausen 2010). Described phosphogenesis was primarily mediated by microbial activity (Álvaro and Clausen 2010; Devaere et al. 2014). It contains an abundant skeletal microfauna (helcionellids, ?polyplacophors, problematic molluscs, orthothecid hyoliths, problematic tubes, and some problematica), Terre-neuvian in age (Nemakit–Daldynian to Tommotian of the Siberian Chart; Devaere et al. 2013) based on the presence of *Oelandiella korobkovi* Vostokova, 1962, *Xianfengella prima* He and Yang, 1982, *Siphogonuchites triangularis* Qian, 1977, *Halkieria operculus* (Qian, 1984), *Lomasulcachites macrus* Qian and Jiang in Luo et al., 1982, *Paragloborilus subglobosus* Qian, 1977, *Pseudorthis acuticincta* Cobbold, 1935, *Paracarinachites sinensis* Qian and Jiang in Luo et al., 1982, *Protoconus orolgainicus* (Zhegallo in Esakova and Zhegallo, 1996) and *Purella gracilis* (Zhegallo in Voronin et al., 1982), and which includes the specimen described herein.

Material and methods

In total, 170 phosphatic partial to complete internal moulds of disarticulated valves of the newly defined species *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov., seven of which with completely to partially preserved external coating, were recovered from the abundant and diverse phosphatic microfauna of the *Heraultia* Limestone, previously described by Cobbold (1935) and Kerber (1988), and recently revised by Devaere et al. (2013). Three of the four studied field-sections have yielded specimens of the species studied herein: K2 (samples K2/3b, K2/3M2, K2/4b, K2/4s, and K2/6) and K3 (samples K3B/2?, K3T/2c, K3T/2d, K3T/2e, K3T/3a, K3T/4a, and K3T/4b) in the vicinity of Marcou village, northwards to Saint Geniès-de-Varensal and K5 (sample K5/19), along the right margin of the Buisson river, close to a fish farm of Saint-Geniès-de-Varensal (for detailed information and sample repartition in the section, see Devaere et al. 2013). The phosphatised specimens, preserved as internal and/or external moulds, were extracted by ca. 10% acetic acid treatment of the limestone samples. They were picked from residues under a stereo-microscope, then studied with a Zeiss Supra 40 VP Scanning Electron Microscope at the Freie Universität Berlin, Zeiss Supra 35 VP Scanning Electron Microscope at the University of Uppsala and a FEI Quanta 200 at the University Lille 1. Figured specimens are housed in the palaeontological collections of the University Lille 1. The terminology used herein follows Williams et al. (1997).

Systematic palaeontology

(Devaere, Holmer, and Clausen)

Incertae sedis

Organophosphatic, bivalved stem-group brachiopods
Mickwitziids [incl. the family Mickwitziidae
Gorjansky, 1969]

Remarks.—We follow the practice by Holmer and Popov (2007: 2581) in recognising the informal grouping of mickwitziid-like stem-group brachiopods, pending further detailed phylogenetic study.

Genus *Kerberellus* Devaere, Holmer, and Clausen nov.

Etymology: In honour of Martin Kerber, palaeontologist, who furnished the first intensive study of the *Heraultia* Limestone.

Type species: *Kerberellus marcouensis* Devaere, Holmer, and Clausen sp. nov., see below; monotypic.

Diagnosis.—As for type species (by monotypy).

Stratigraphic and geographic range.—As for type species.

Kerberellus marcouensis Devaere, Holmer, and Clausen sp. nov.

Figs. 2–8.

Etymology: From the village of Marcou, the type locality.

Type material: Holotype: ventral valve USTL1234-5 (Fig. 4B), sample K3T/2e. Paratypes: ventral valve with external coating USTL2856-3 (Fig. 2C), dorsal valves: USTL2856-6 (Fig. 6A), USTL2860-5 (with external coating, Fig. 6B), USTL2856-1 (juvenile form, Fig. 8B), sample K2/4s.

Type locality: K3 section, along D52 road, north to the village of Marcou, Hérault, France.

Type horizon: *Heraultia* Member, Marcou Formation, Cambrian Stage 2 (*Watsonella crosbyi*–*Oelandiella korobkovi* Zone).

Material.—170 phosphatic partial to complete internal moulds including figured specimens: USTL1231-6, 1232-1, 1232-3–5, 1261-12, 2856-1, 2856-3, 2856-5, 2856-6, 2857-1, 2857-6, 2857-8, 2858-1, 2858-2, 2858-4, 2859-2–7, 2860-2, 2860-4–6, 2861-6, and 2862-1.

Diagnosis.—Ventribiconvex and inequivalved bivalved shell ovate to subcircular in outline. Radially-aligned, smooth, cylindrical to hour-glass shaped canals running orthogonally throughout entire thickness and surface of the valves except for the sub-apical planar field (interarea) which lacks perforations. Mixoperipheral growth of both valves. External surface of the shell with radial and possibly comarginal wavy ornamentations, sometimes pustulose. High conical ventral valve with subcentral to submarginal apex possibly curved over the posterior margin. Ventral interarea apsacline to catacline. Low conical dorsal valve with marginal apex, dorsal interarea catacline to anacline.

Description.—The bivalved, bilaterally symmetrical shell (median plane normal to the commissure) is ventribiconvex and inequivalved, ovate to subcircular in outline. It is com-

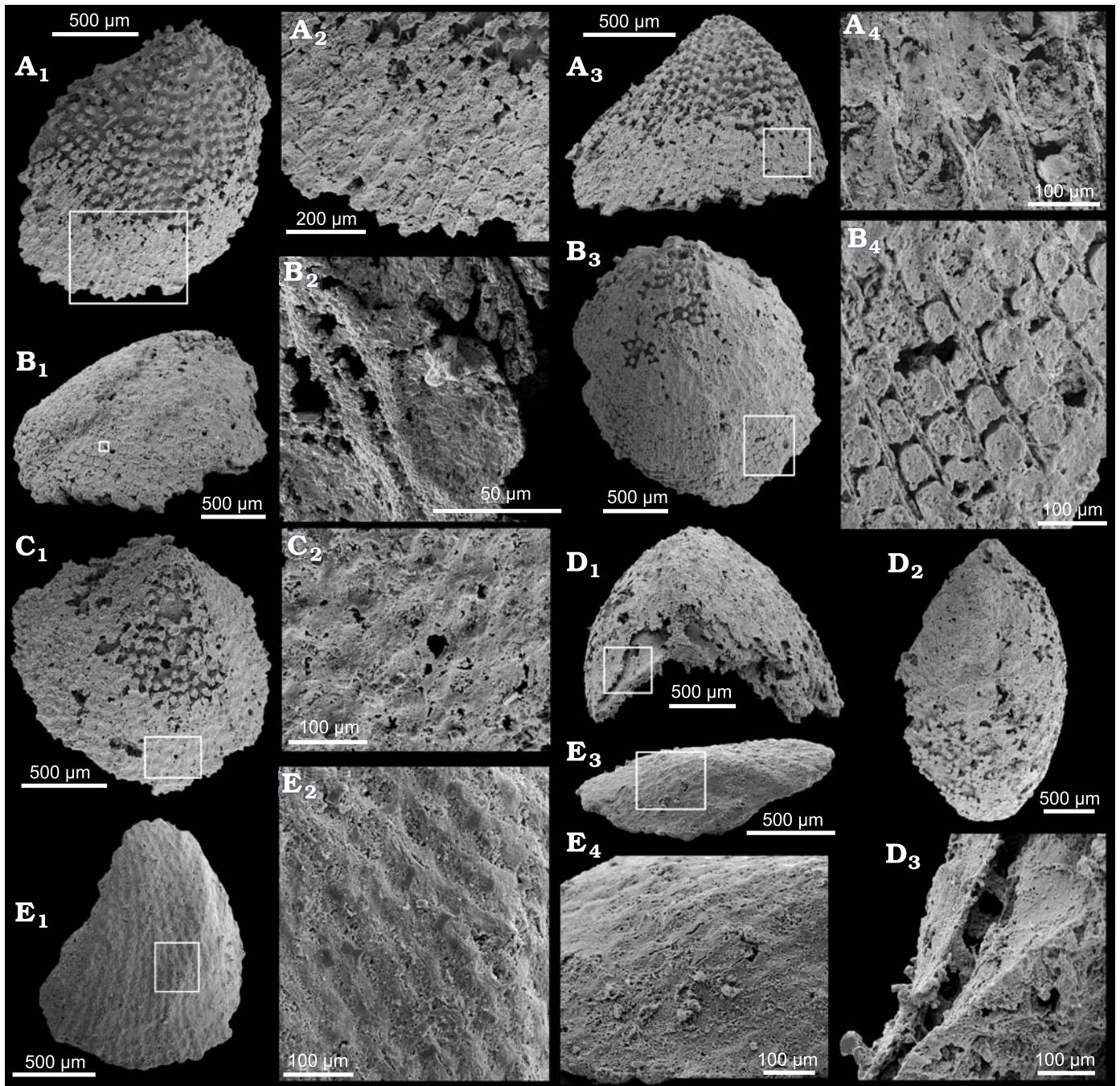


Fig. 2. Mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL2859-7; A₁, external view of a ventral valve; A₂, detail of A₁, anterior marginal area with partially preserved external coating; A₃, anterior view of a ventral valve; A₄, detail of A₃, external coating organised into radial furrows and ribs alternatively. **B.** USTL2857-6; B₁, lateral view of ventral valve with external coating; B₂, detail of B₁, ridge between radial rows of pores damaged, giving the shell a radial striated pattern; B₃, external view of ventral valve with external coating; B₄, detail of B₃, partially preserved external coating with damaged ridge between rows of pores. **C.** USTL2856-3 (paratype); C₁, external view of a ventral valve; C₂, detail of C₁, pustulose external mould (costae crossed by comarginal ribs). **D.** USTL2861-6; D₁, posterior view of a ventral valve with thick external coating; D₂, external view of ventral valve with external coating; D₃, detail of D₁, phosphatic internal moulds of pores running from the internal mould to the external coating. **E.** USTL1232-3; E₁, external view of external mould; E₂, detail of E₁, sinuous radial costae associated with comarginal ribs; E₃, lateral view of external mould; E₄, detail of E₃, external mould with ridges damaged.

posed of a high conical ventral valve (height/diameter ratio up to 1/2) and a low conical dorsal valve (height/diameter ratio up to 4/5).

Some specimens exhibit a phosphatic external coating which mimics the external surface of the shell (Fig. 2). In

most cases, this latter displays radial wavy costate ornamentation: the furrows correspond to rows of radial structures interpreted herein as coated and filled canals (or tubes according to Balthasar 2004; Skovsted and Holmer 2003; Skovsted et al. 2010; see below) alternating with ridges (Fig. 2A).

The summit of the ridges of the external-coating is generally damaged (Fig. 2E₃, E₄), resulting in sections appearing as a radial, striated pattern (Fig. 2B). On some specimens, the costae are crossed by comarginal ribs and the external mould exhibits low rounded pustules at the intersection between costae and ribs (Figs. 2C, E). The radial costae have a sinuous appearance when associated with comarginal ribs (Fig. 2E). In thick external coatings, the external, wavy, radial structure is no longer visible (Fig. 2D).

All internal moulds of valves exhibit radially-aligned extensions (30 to 65 µm in diameter; Fig. 3A₁, B₁, G₁, H₁, K₁) oriented perpendicular to their surface (inner shell surface; Fig. 2D₃). Such structures are interpreted herein as preserved tubes (canals) piercing the shell. Canals are cylindrical to hour-glass shaped in lateral view (Figs. 3A₂, B₂, K₂, 5E₂, 8C₆) with circular to rarely almost polygonal (taphonomic?) outer, transverse section (Figs. 3A₂, 5B₁, 7A₂). Their lateral surfaces are smooth (Figs. 3A₂, B₂, I₂, I₃, K₂, 5E₂, 8C₆). They are preserved as phosphatic peripheral coating (Fig. 3H₂-J₂) which is most often massively filled (Fig. 3K₂), even if in some areas the tubes are partly hollow (Fig. 3H₂). The peripheral coating of the canals is variably thick (Fig. 3H₂, I₂, I₃, J₂). Massive moulds of the canals have a concave outer extremity (Figs. 3A₂, 5E₂). The rows of canals extend from the apex to the apertural margin (Figs. 4A₁, B₁, 5B₁, C₁, D₁, 6A₁, 7A₁, D₁, E₁). During growth, new rows are inserted distally between previous ones (lower arrows in Figs. 4A₂, C₂, 7A₂).

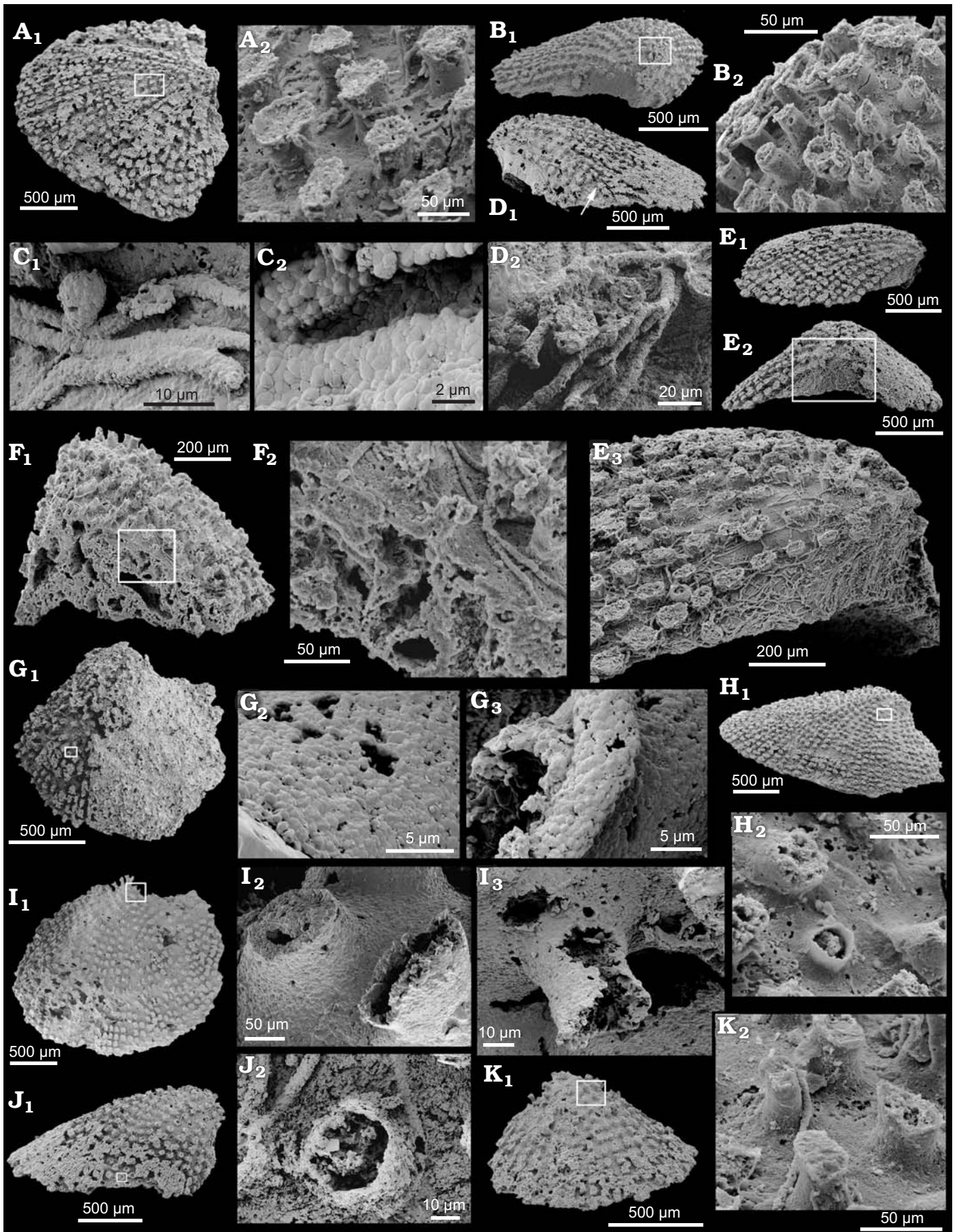
27 of the 47 identifiable valves are ventral (Figs. 4, 5). In ventral view, the ventral valves are oval, either wider than long (Figs. 4B₁, C₁, 5C₁, E₁) or longer than wide (Figs. 4A₁, 5B₁) to circular in outline (Fig. 5A₁, D₁). In lateral view, the ventral valves are strongly conical to pyramidal (Figs. 4A₆, B₂, C₃, 5A₂, C₄, D₃) with the lateral faces almost planar. The apertural surface is planar to slightly convex. No clue of a differentiated juvenile shell is observed (Fig. 4A₂, C₂). The ventral apex is submarginal and sometimes curved over the posterior margin (Figs. 4A₃-A₆, B₂, C₃, 5A₃, B₂). In some specimens, rows of canals are laterally offset from a line crossing the ventral apex down to half way to the anterior commissure; this strip, which is depleted of canals, is sometimes underlined by a shallow furrow on the internal mould (median low-keel in the shell; upper arrows in Figs. 4A₂, C₂, 5F). In other specimens, closely arranged radial rows of canals go up to the apex and some pairs of apical canals are almost joined together at their inner extremity (Fig. 5E₁-E₃). The ventral posterior margin varies from rectilinear (Fig. 4A₁-C₁) to obtuse-angled (sometimes re-entrant, with lateral lobate extremities; Fig. 5A₁-E₁) in upper view. The ventral interarea is devoid of canals (Figs. 4A₃, A₄, B₃, C₃, 5A₂, A₃, B₂, C₂, C₃, D₂, D₄, F₁) and its internal mould generally exhibits a triangular depression below the apex (Figs. 4C₃, 5A₃, C₃) rarely duplicated by a posterior prominent extension (Figs. 4B₂, 5D₄). The ventral interarea is apsacline to catacline. In some specimens, its commissural margin is notched by an angular sinus located below the apex (Fig. 4A₃, B₃, C₃) or is almost rectilinear (Fig. 5A₂, C₂, D₂, F). The growth of the ventral valve is mixoperipheral.

The dorsal valves correspond to 17 of the 47 identifiable valves. They are oval (Figs. 6A₁, B₁, 7A₁, E₁) to subcircular (Fig. 7B₁-D₁) in dorsal view. The oval forms are either longer than wide (Fig. 6B₁) or wider than long (Figs. 6A₁, 7A₁, E₁). In lateral view, the valves are almost planar (Figs. 6A₃, 7A₄, B₂, B₄, E₂) to very low conical (Figs. 6B₂, 7C₃, D₃). The apex is marginal (Figs. 6A₆, B₂, 7A₃, B₄, D₃, E₄). No trace of differentiated juvenile shell is identified (Figs. 6A₂, 7A₂, E₃). The posterior margin varies from rectilinear (Fig. 7B₁, C₂, D₁, E₁) to acute in upper view, the left and right extremities of the posterior margin being displaced posteriorly (Figs. 6A₁, B₁, B₆, 7A₁). The interarea shows a median, subapical sinus that notches the interarea commissural margin (Figs. 6A₄, A₅, B₄, B₆, 7A₃, C₃, C₄, D₃, E₃). The interarea is sometimes stepped with a shelf-like subapical part (Fig. 8D₂-D₄) and a posterior, poorly defined, catacline to anacline part. The growth is mixoperipheral but the subapical growth is very limited.

Three out of the 47 identifiable valves, corresponding to smaller specimens (half of the mean size of shells; Fig. 8), have a smaller number of relatively larger canals (compared to their general size). They may represent juvenile specimens of dorsal valves based on their planar shape (Fig. 8A₆, B₆, B₇) and the interarea commissural margin sinus (Fig. 8A₂, B₄, C₂, C₄). The apex is subcentral (Fig. 8A₁) to marginal (Fig. 8B₁, C₁). Their interarea is hypercline. In specimens with subcentral apex, the subapical field is organised into a shelf (Fig. 8A₁-A₄). In the other specimens, the interarea exhibits a step-like structure (Fig. 8B₂, B₃, C₂-C₄).

Remarks.—The ontogeny of *K. marcouensis* can be inferred from the juvenile (Fig. 8A) and intermediate forms (Figs. 7D, 8B, C). The juvenile specimens of dorsal valves exhibit a hypercline interarea forming a subapical shelf (Fig. 8A₁-A₅). During growth, the interarea develops a distal catacline portion (Fig. 8C₂-C₄, C₆) which results in a stepped subapical field (Fig. 8B₂-B₄). In adult specimens, the interarea becomes apsacline but generally retains traces of the step-like structure (Fig. 7D₂-D₄).

This species was originally described by Kerber (1988) under open nomenclature as *Dictyonina?* sp. Species of the Cambrian paterinate brachiopod *Dictyonina* are characterised by having fine radiating rows of subhexagonal pits, increasing in size distally (see Laurie 2000: 152). Kerber (1988) interpreted the radial structures in the present specimens as representing moulds of the radiating rows of subhexagonal pits in *Dictyonina*. However, *Dictyonina* and *Kerberellus* only share superficial similarities. *Kerberellus* is characterised by large radial ovoid, hour-glass shaped extensions of taphonomic origin which are interpreted herein as tubes (canals) or punctae running through a thick organic shell (see below) whereas the fine radiating rows in *Dictyonina* correspond to subhexagonal pits in the organophosphatic shell. Moreover, in *Dictyonina* the thin shell is densely depressed (net-like) and walls of adjacent depressions are contiguous. In *Kerberellus*, canals are separated by relatively large shell areas. Finally, the smooth, integral subapical area of *Kerber-*



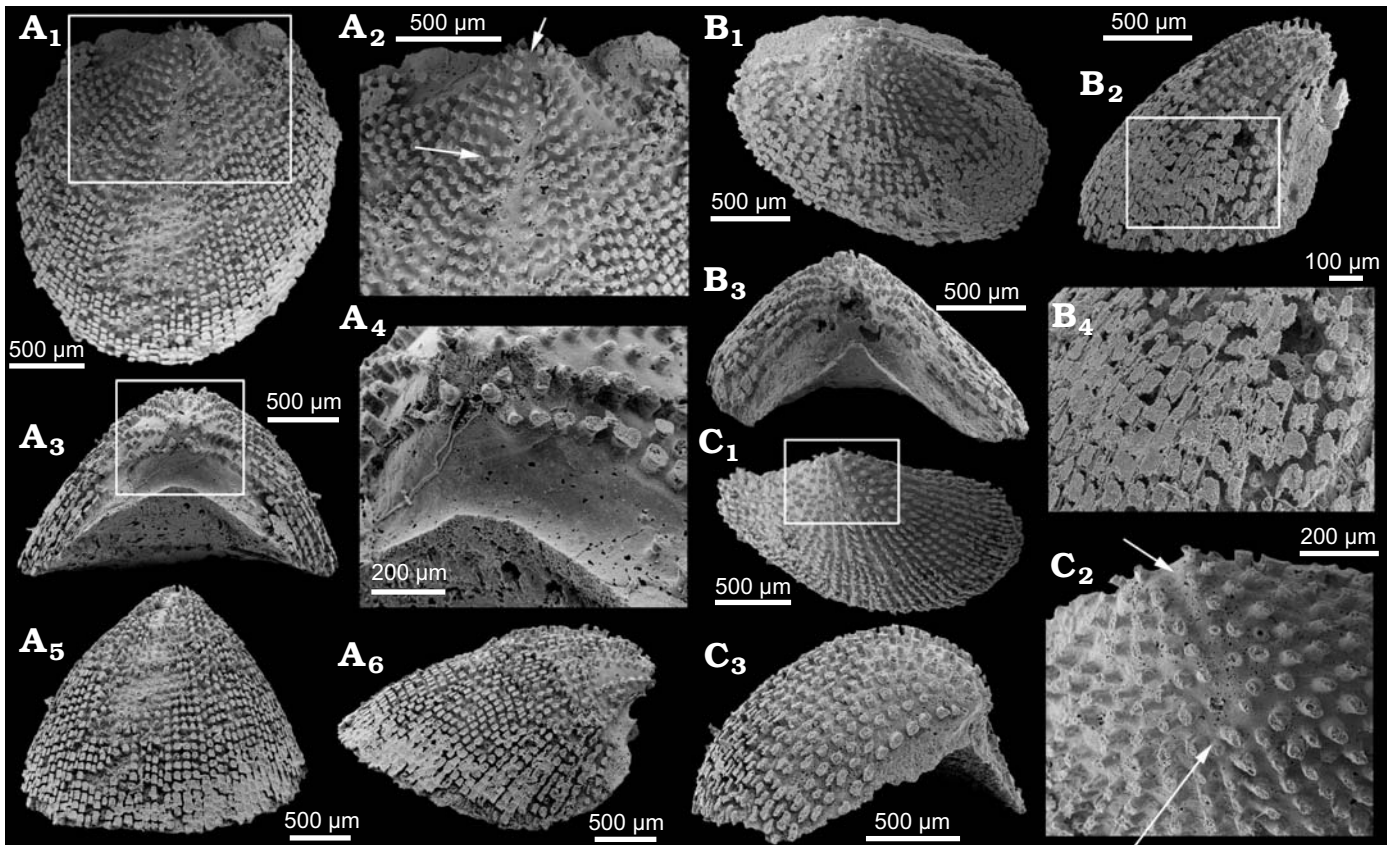


Fig. 4. Ventral valve of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL2859-6; A₁, external view; A₂, detail of A₁, apical area, upper arrow pointing median furrow crossing internal mould of apex, lower arrow pointing new row of pores inserted between existing rows; A₃, posterior view; A₄, detail of A₃, interarea with triangular sinus of the subapical margin; A₅, anterior view. A₆, Lateral view of highly conical ventral valve. **B.** USTL1234-5 (holotype); B₁, external view; B₂, lateral view of highly conical ventral valve; B₄, detail of B₂, partially preserved external coating with variable of tubes distal end and long, radial, straight and thin phosphatic sheets running from the apex to the anterior margin between rows of radial tubes; B₃, posterior view, interarea with triangular sinus of the subapical margin. **C.** USTL2860-6; C₁, external view; C₂, detail of C₁, apical area, upper arrow pointing median furrow crossing internal mould of apex, lower arrow pointing new row of pores inserted between existing rows; C₃, postero-lateral view, interarea with triangular depression.

ellus is most probably a clue of the absence of deltidial plates whereas the paterinid *Dictyonina* has a homeodeltidium.

Khasagtina primaria Ushatinskaya, 1987 is superficially similar to *K. marcouensis* although the former exhibits an apical foramen on ventral valves and lacks the canals extending through the shell of the latter (but the preservation and low number of specimens may bias these observations). Both species exhibit radial costae but *K. primaria* lacks the

comarginal ribs observed in *K. marcouensis*. The interarea of the ventral valves of *K. primaria* are apsacline as in *K. marcouensis* (although it is catacline in some specimens) and they both exhibit obtuse-angled, re-entrant, posterior margins with lateral lobate extremities. However, the ventral interarea of *K. primaria* exhibits traces of pseudodeltidium the presence of which cannot be demonstrated in *K. marcouensis*. The dorsal catacline interarea of both species is

← Fig. 3. Preservation of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL1232-1; A₁, oblique lateral view of dorsal valve; A₂, detail of A₁, tubes with smooth uniseriate microbial filaments. **B.** USTL2856-5; B₁, posterior view of ventral valve; B₂, detail of B₁, smooth uniseriate microbial filaments at the top of the tubes (beneath the original shell surface). **C.** USTL2859-5; C₁, microbial filaments; C₂, detail of C₁, packed angular to spheroid phosphatic grains constituting the microbial filaments. **D.** USTL2859-7; D₁, lateral view of ventral valve, arrow pointing D₂; D₂, detail of D₁, branching microbial filaments. **E.** USTL2860-2; E₁, lateral view of ventral valve; E₂, posterior view of ventral valve; E₃, detail of E₂, interarea intensively colonised with euendolithic microorganisms. **F.** USTL1231-6; F₁, broken specimen; F₂, detail of F₁, porosity in the loose organisation of the phosphatic clusters of internal moulds. **G.** USTL2862-1; G₁, External view of unidentified valve; G₂, detail of G₁, thin and smooth microbial biofilm corresponding to the amalgamation of angular to spheroid phosphatic bodies coating the internal surface of the original shell; G₃, microbial filament and tube constituted of similar packed angular to spheroid phosphatic grains. **H.** USTL1232-4; H₁, lateral view of dorsal valve; H₂, detail of H₁, hollow tube, the preservation of which corresponds to a thin microbial film coating the internal part of what corresponded to a pore. **I.** USTL2858-1; I₁, external view of dorsal valve; I₂, detail of I₁, hollow tube, the preservation corresponds to a thick microbial film coating the internal part of what corresponded to a pore; I₃, partly filled tube. **J.** USTL2859-7; J₁, lateral view of ventral valve; J₂, Detail of J₁, apatite infill at base of tube. **K.** USTL2856-1 (paratype); K₁, oblique anterior view of dorsal valve; K₂, detail of K₁, smooth lateral surface of tubes and microbial filament running between tubes.

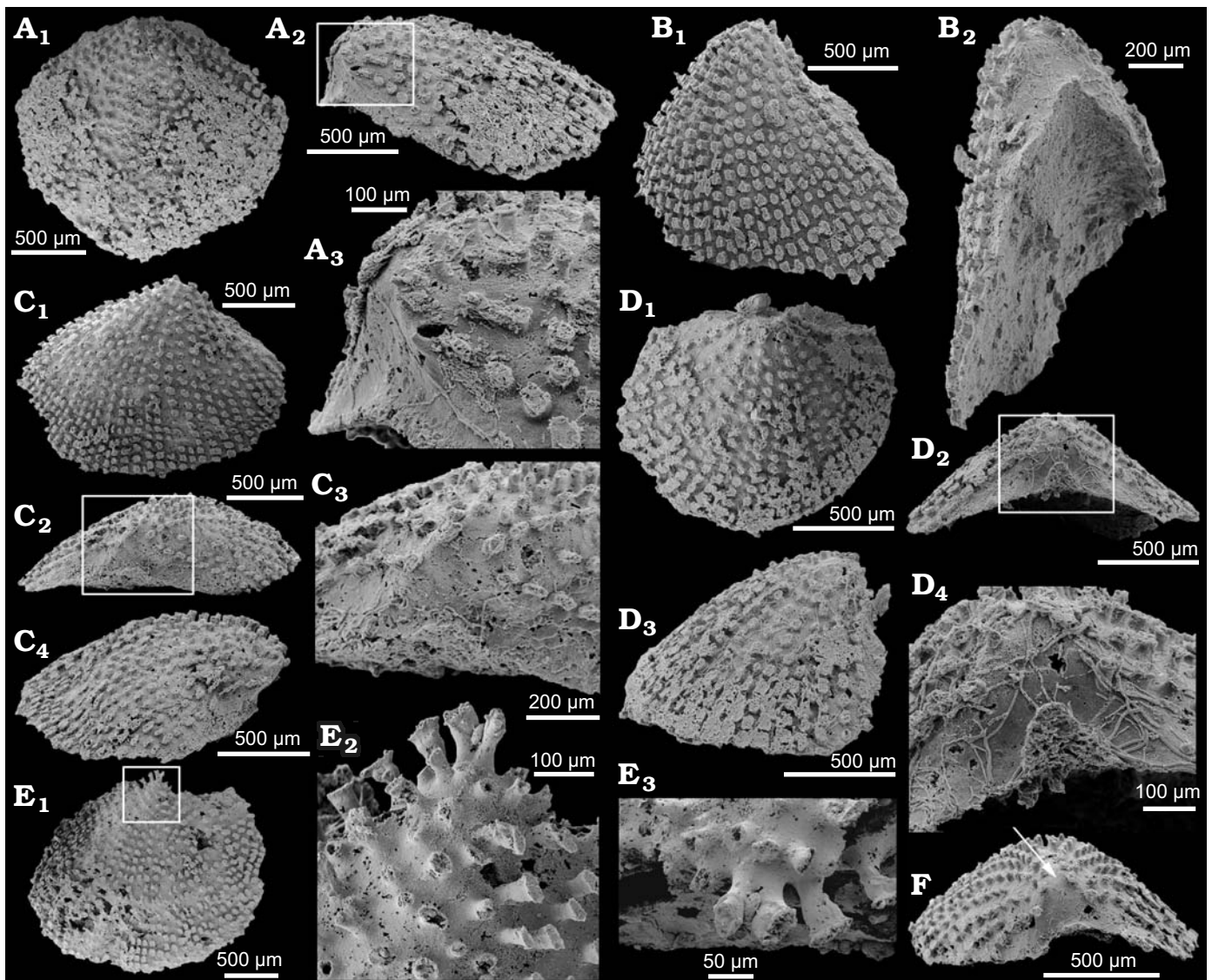


Fig. 5. Ventral valve of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL2859-5; A₁, external view; A₂, postero-lateral view; A₃, detail of A₂, interarea with triangular depression. **B.** USTL2856-5; B₁, external view; B₂, posterior view, interarea with triangular sinus of the subapical margin. **C.** USTL2859-3; C₁, external view, squared area magnified in C₂; C₂, posterior view; C₃, detail of C₂, internal mould of interarea with subapical triangular depression; C₄, lateral view. **D.** USTL2858-4; D₁, external view; D₂, lateral view; D₃, posterior view; D₄, detail of D₃, interarea with internal mould of prominent triangular structure. **E.** USTL2858-1; E₁, external view; E₂, detail of E₁, apical area, pair of closely spaced tubes at the apex; E₃, detail of E₁, posterior area, pair of closely spaced tubes at the apex. **F.** USTL2859-4; posterior view, arrow pointing median furrow crossing internal mould of apex.

acute (incurved), with the left and right extremities of the posterior margin displaced posteriorly.

Massive, taphonomically-controlled extensions seen in some internal moulds of *K. marcouensis* (interpreted as filled canals) can be compared with radial rows of tubercles of *Psamathopalass amphidoz* Liu, 1979. This latter species was regarded by Liu (1979) as a possible brachiopod although it is too poorly understood to be confidently assigned to any phyla according to Williams et al. (1997). One of the authors (LEH) restudied the type material of *P. amphidoz* and concluded that it corresponds to a pustulose cone lacking brachiopod characters. Therefore, the pustules of *P. amphidoz* clearly differ from the processes described

in *Kerberellus* which are not primary structures but taphonomically controlled structures.

Stratigraphic and geographic range.—*Heraultia* Member, Marcou Formation, Cambrian Stage 2 (*Watsonella crosbyi*–*Oelandiella korobkovi* Zone), proximity of the villages of Marcou (K2, K3) and Saint-Geniès-de-Varensal (K5), Hérault, France.

Preservation and shell structure

The specimens are preserved as phosphatic coatings and moulds of disarticulated valves; therefore, the original

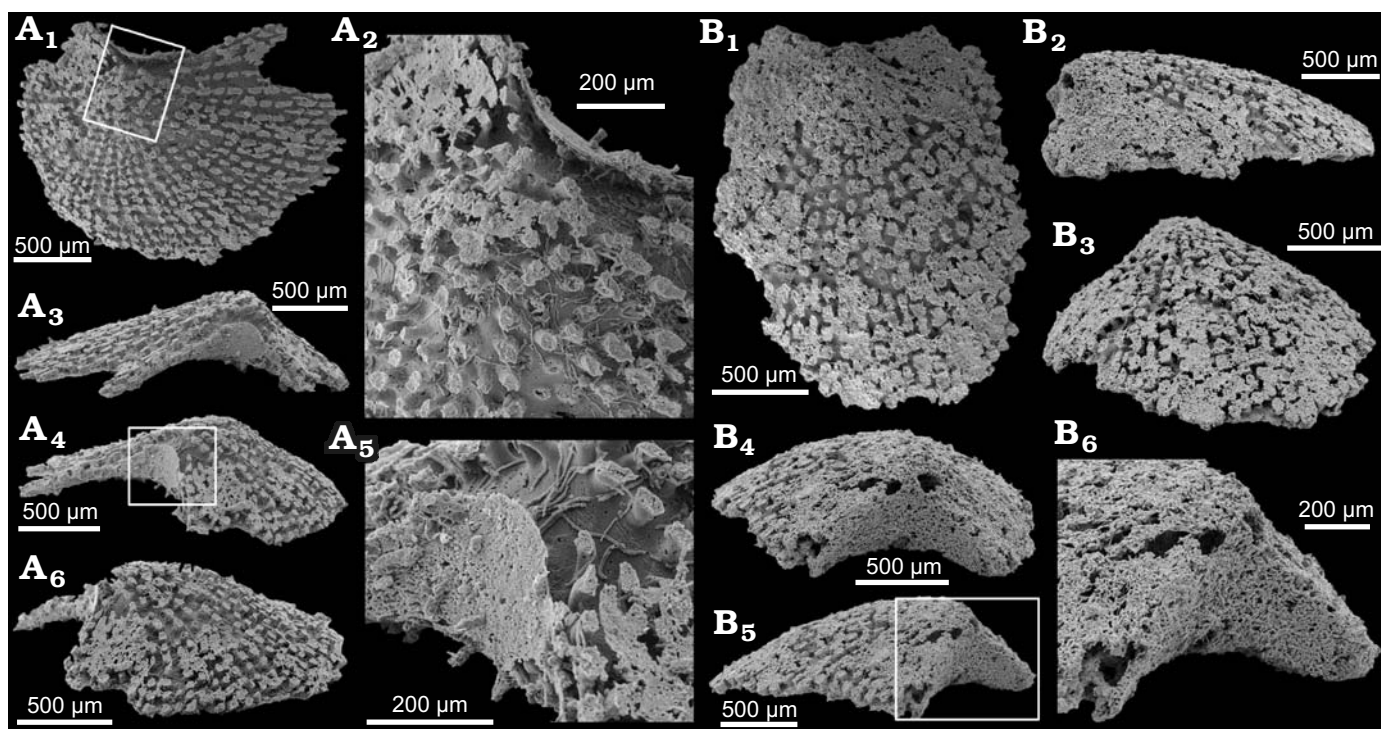


Fig. 6. Dorsal valve of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL2856-6 (paratype); A₁, external view; A₂, detail of A₁, apical area; A₃, posterior view; A₄, postero-lateral view; A₅, detail of A₄, interarea; A₆, lateral view of planar dorsal valve. **B.** USTL2860-5 (paratype); B₁, external view; B₂, lateral view; B₃, anterior view; B₄, posterior view; B₅, postero-lateral view; B₆, detail of B₅, external coating of interarea with angled posterior margin creating a subapical sinus.

structure of the shell is no longer observable. The original chemical composition of the shell might have been largely organic with possible phosphatic mineralisation as inferred by Skovsted and Holmer (2003) and Skovsted et al. (2010) for the mickwitziid *Setatella significans* Skovsted, Streng, Knight, and Holmer, 2010. However, a partly calcareous composition (the calcareous material then dissolved during acetic acid treatment) cannot be ruled out (see also Skovsted and Holmer 2003: fig. 3). The organic or poorly mineralised material would have been coated and filled by phosphatic material prior to decay (Fig. 9); and the tubular structures in *Kerberellus* may represent the outer coating and infill of tubular walls or canals (cf. Skovsted and Holmer 2003: fig. 14). The preservation of the filling of digestive tracts in orthothecid hyoliths co-occurring in some levels with *K. marcouensis* (K2/4b, K2/4s, K2/6, K3T/2c, K3T/2e, K3T/4a, K3T/4b, and K5/19) argues for an early microbially mediated phosphatisation (Devaere et al. 2014) compatible with a phosphatic coating and infill of a mostly organic-walled shell. Most of the fossils extracted from the *Heraultia* Limestone consist of phosphatic internal moulds, which, in most cases, prevent any probing observation of the internal coating of the shell (Devaere et al. 2013). The recovered material from the *Heraultia* Limestone does not include original phosphatic remains. Original calcareous shell material is generally visible in thin sections, most often recrystallised. However, available thin sections do not include specimens of *Kerberellus* which are relatively rare in the preserved assemblage. Although phosphatic internal

mould and coating are common in the *Heraultia* Limestone, phosphatic replacement of the original shell is rarely observed (Clausen and Álvaro 2007). Rare cases of limited phosphate replacement of calcareous hyolith shells have been reported by Clausen and Álvaro (2007: fig. 5). Phosphatised shell material, even to some degrees, has not been recovered in *K. marcouensis* which is preserved as internal mould and internal and external phosphate coating. Moreover, the phosphatisation of carbonate shell is generally preceded by the dissolution of the carbonate material leading to its surface natural etching (Balthasar 2008). Such a process is accompanied by a replication of the original shell microstructure by phosphate (Kouchinsky and Bengston 2002). The surface of the shell coating of *K. marcouensis* does not exhibit neither traces of original shell dissolution, nor shell microstructure replication. This further argues for an original organic shell rather than calcareous. Finally, the shell of phosphatic brachiopods are organised into alternating laminations of apatite granules, glycosaminoglycans and collagen or chitin (Williams et al. 1997). Very early diagenetic remobilisation of original apatite within shell laminae can occur and phosphate is sometimes reorganised along organic layers that acted as nucleation surfaces for apatite cements (Balthasar 2007). Such a process has been observed in *Setatella significans* Skovsted, Streng, Knight, and Holmer, 2010 by Skovsted and Holmer (2003) and Skovsted et al. (2010) or *Mickwitzia muralensis* Walcott, 1913 by Balthasar (2004). In those specimens, transversal striations on the walls of orthogonal tubes corresponding to

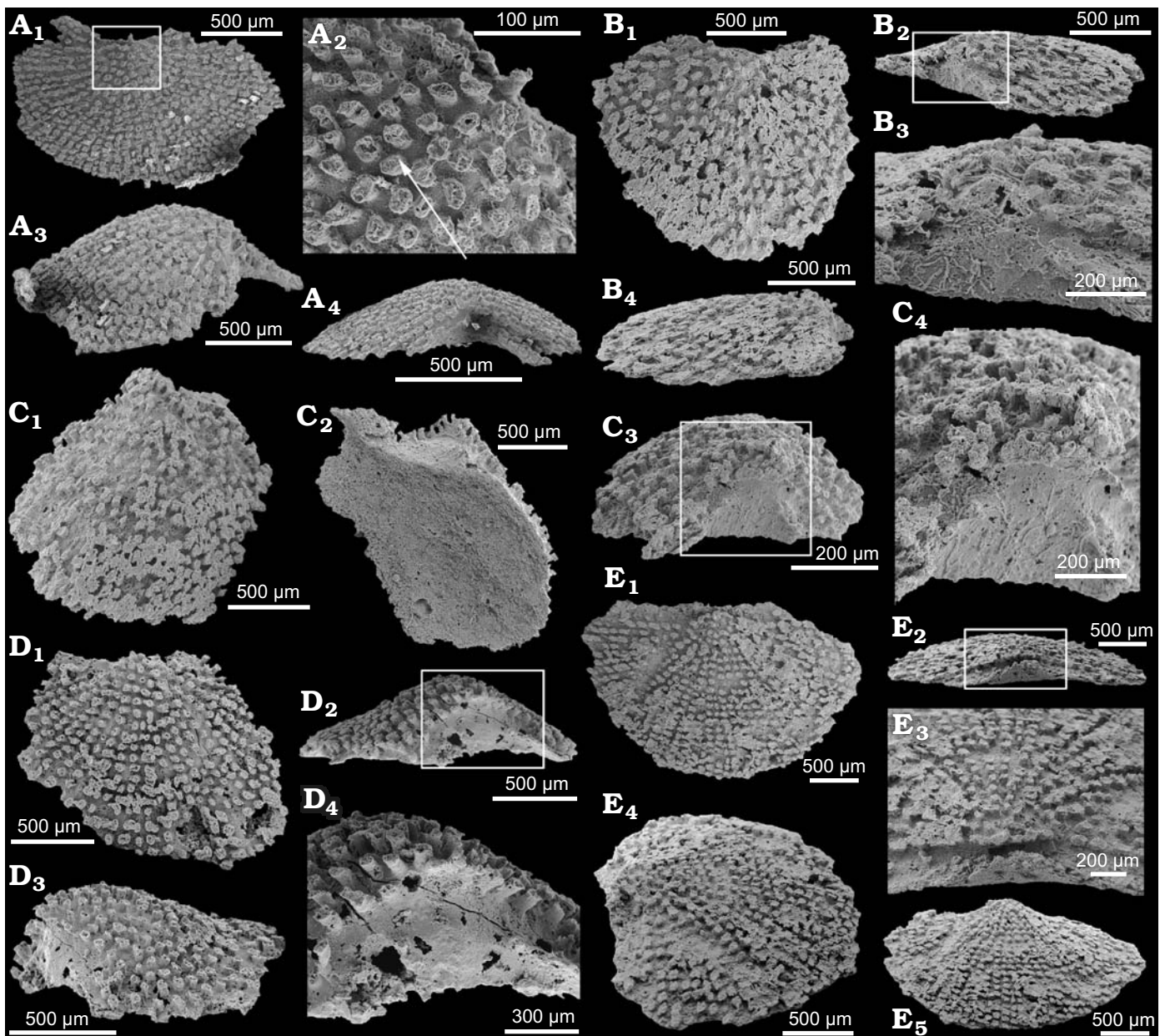


Fig. 7. Dorsal valve of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL1261-12; A₁, external view; A₂, detail of A₁, apical area, arrow pointing new row of pores inserted between existing rows; A₃, postero-lateral view; A₄, posterior view. **B.** USTL2857-8; B₁, external view; B₂, postero-lateral view; B₃, detail of B₂, internal mould of interarea; B₄, lateral view of planar dorsal valve. **C.** USTL2858-2; C₁, external view; C₂, internal view; C₃, posterior view; C₄, detail of C₃, internal mould of interarea. **D.** USTL2859-2; D₁, external view; D₂, posterior view; D₃, postero-lateral view; D₄, detail of D₂, interarea. **E.** USTL1232-1; E₁, external view; E₂, posterior view; E₃, detail of E₂, apical area and interarea; E₄, lateral view of planar dorsal valve; E₅, anterior view.

the secondary phosphate layers are preserved. If a similar process occurred in *K. marcouensis*, comparable transversal striations should be observed on the internal moulds of the canals even if the phosphate layers were not preserved. Therefore, the absence of phosphate layers and of their traces on the canal moulds of *K. marcouensis* strengthens the interpretation that the shells were not originally phosphatic but most probably organic.

The surface of the internal moulds from the *Heraultia* Limestone, including *Kerberellus* specimens, is infested by smooth uniseriate (Fig. 3A₂, C₁, F₂) to dichotomously

branched (Fig. 3D₂) phosphatic filaments (2–50 µm in diameter) attesting for intense microbial activity (Fig. 3A–E). Densely distributed phosphatic filaments at the surface of the internal moulds (Fig. 3E₂, E₃) of *Kerberellus* suggest the shell may have been intensively colonised by shell-perforating microbial organisms which perforations have been phosphatised simultaneously to shell coating (Clausen and Álvaro 2007; Álvaro and Clausen 2010). The filaments are made of packed angular to spheroid phosphatic grains (Fig. 3C, G₃). The internal surface of the shell is generally coated with a relatively thin crust most probably made by amalgamation

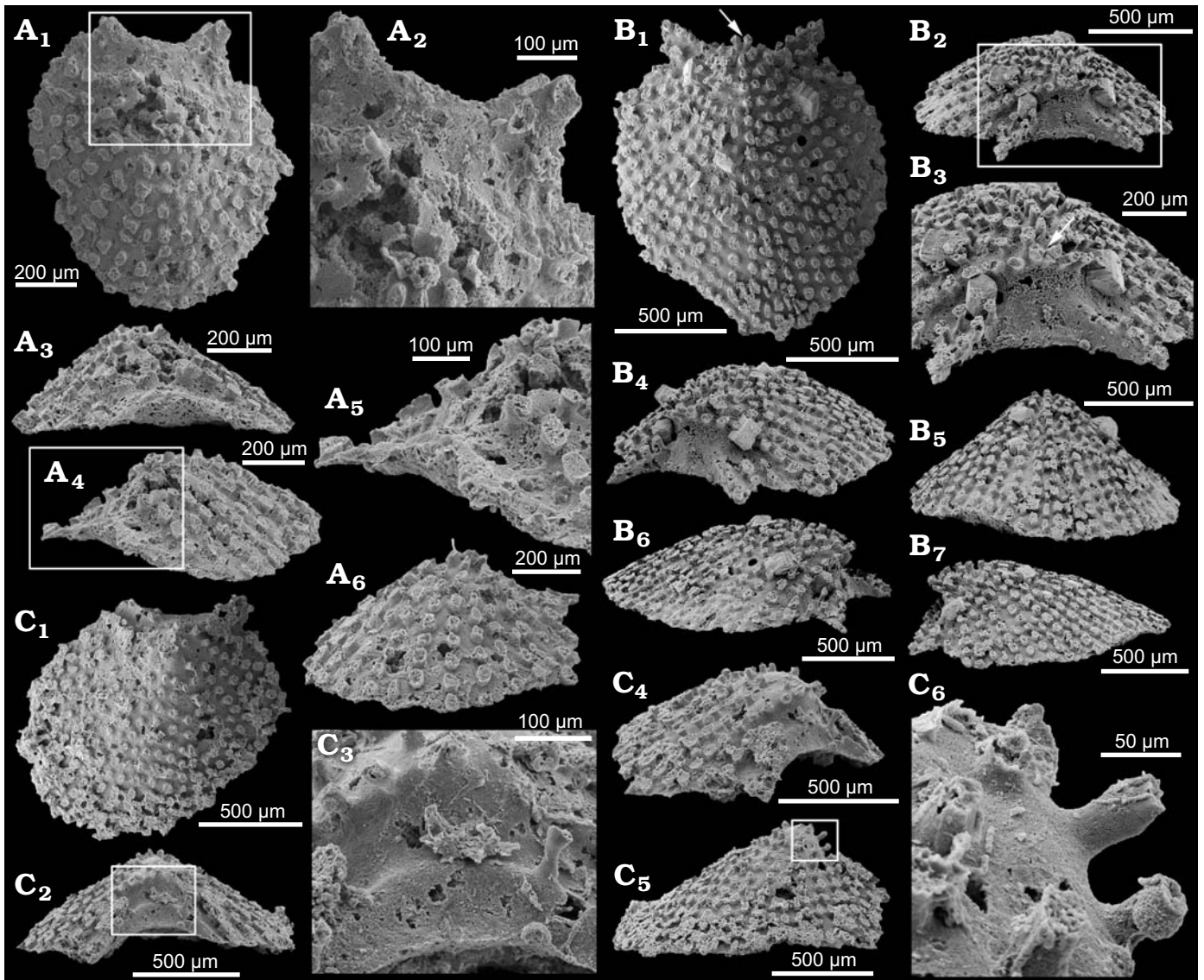


Fig. 8. Juvenile specimens of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. from the Terreneuvian *Heraultia* Member, Montagne Noire (southern France). **A.** USTL2857-1; A₁, external view; A₂, detail of A₁, apical area and interarea; A₃, posterior view; A₄, postero-lateral view; A₅, detail of A₄, interarea organised into subapical shelf; A₆, antero-lateral view. **B.** USTL2860-4; B₁, external view; B₂, posterior view; B₃, detail of B₂, internal mould of interarea, arrow pointing the two close tubes; B₄, postero-lateral view; B₅, anterior view; B₆, B₇, lateral views. **C.** USTL2856-1 (paratype); C₁, external view; C₂, posterior view; C₃, detail of C₂, internal mould of interarea with step-like structure; C₄, postero-lateral view; C₅, antero-lateral view; C₆, detail of C₅, long and smooth apical tubes.

of angular to spheroid phosphatic, microbial bodies (Fig. 3G₁, G₂, I₂) or by very thin and smooth crust of phosphate corresponding to an early diagenetic coating of the original shell (Fig. 3H₂, J₂). The internal moulds consist of a loose network of botryoidal clusters that occlude the cavities inside internal coatings of shells (Fig. 3F). The loose organisation of the phosphatic clusters induces the presence of porosity originally filled with calcite cement (Fig. 3F₂). Some specimens also exhibit a phosphatic external coating reproducing the external aspect of the original shell. The canal sections allow the description of a primary phosphatic coating of the shell, followed by an infill by phosphatised lime and debris. The phosphatic internal coating extends into the outer coating of the shell (Fig. 9).

Concluding remarks

Kerberellus marcouensis Devaere, Holmer, and Clausen gen. et sp. nov. is herein tentatively assigned to brachiopods. Two distinct morphotypes are described which argue for a bivalved shell, bilaterally symmetrical with median plane normal to commissure. Based on their preservation pattern, processes are interpreted herein as secondary infill or inner coating of tubes (canals) piercing the entire thickness of the shell (Fig. 2D₃). They can be compared either to endopunctae or pores of brachiopods. An irregular lateral wall and connections to the exterior of the shell by a brush of nanometer-sized tubes in terebratulids (called canopy) or by micrometer-sized branching tubes perforating the primary shell layer in craniids

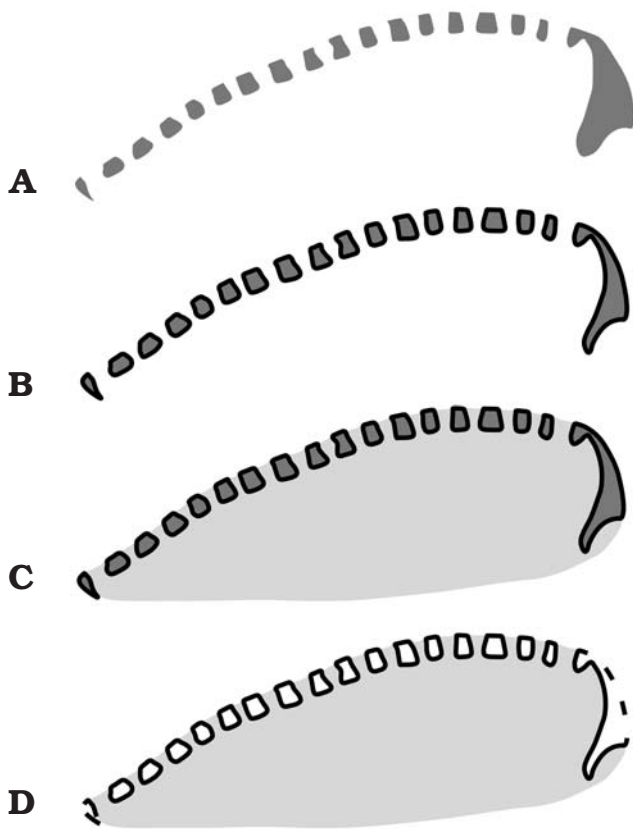


Fig. 9. Preservation stages of mickwitziid *Kerberellus marcouensis* Devaere, Holmer, and Clausen gen. et sp. nov. in the *Heraultia* Limestone from the Montagne Noire (southern France). **A.** Original shell in dark grey. **B.** Phosphatic inner and outer coating of the shell, black line. **C.** Second phosphatisation phase with phosphatisation of lime and cementation of debris. **D.** Decay of original organic material of shell (and/or dissolution of possible original or of secondary diagenetic origin shell carbonate material during acetic acid treatment [see Clausen and Alvaro 2007; Alvaro and Clausen 2010]).

are characteristic of true endopunctae (Pérez-Huerta et al. 2009). The irregular longitudinal shape rarely observed in the canals of *K. marcouensis* (Fig. 5E₂) might be compared with endopunctae or precursors to endopunctae. However, the external terminations of the canals of *K. marcouensis* differ with characteristic endopunctae by their direct connection with the exterior (Fig. 2D₃) differing from the outer connection of endopunctae through a network of narrower tubes. Such shell penetrating structures are closer to mickwitziid tubes. Therefore, *K. marcouensis* is tentatively interpreted herein as a relative or member of the family Mickwitziidae; a group of organophosphatic, bivalved stem brachiopods (Holmer et al. 2002; Balthasar 2004; Skovsted and Holmer 2003, 2005; Skovsted et al. 2009, 2010). The general shape and pustulose external surface of *Kerberellus* valves are similar to those of mickwitziids. However, the uneven shape of some rare canals of *K. marcouensis* differs from mickwitziids perforations. Furthermore, the perforations described in mickwitziids are generally much smaller (5 to 25 µm) than the canals of the present specimens (30 to 65 µm), which also differ in the absence of longitudinal striations. The coating of the surface of the shell by coarse apatite deposits possibly obscured any

such striation if originally present. However, exquisite details of the shell surface are preserved in the *Heraultia* Limestone, such as polygonal imprints (of 5 µm in diameter) on internal moulds of molluscs, interpreted as replica of a prismatic shell layer (Devaere et al. 2013). In *Setatella significans* Skovsted, Streng, Knight, and Holmer, 2010 (= *Mickwitzia* cf. *occidens* sensu Skovsted and Holmer 2003), which probably belongs to the derived stem group of the Linguliformea, the through-going tubes located in the median area of the shell are not striated (Skovsted and Holmer 2003; Skovsted et al. 2010), whereas longitudinally striated tubes, which are located at the pseudointerarea are oriented within the plane of the laminar shell. Such striated perforations are also present in *Micrina*, a tomotioid belonging to the brachiopod stem group, and are interpreted in *Setatella significans* and *Micrina* as setigerous tubes (Skovsted and Holmer 2003), the striations corresponding to casts of microvilli (Holmer et al. 2002; Williams and Holmer 2002). In studied specimens of *Kerberellus*, canals are absent from the interareas. Moreover, all perforations in *M. muralensis* are non-striated, orthogonally shell-penetrating tubes. Balthasar (2004) pointed out that the only known epithelial pockets in the mantle of brachiopods that could be associated with the smooth orthogonally shell-penetrating pores present in *M. muralensis* are setal follicles. In specimens of *M. muralensis* he studied, the tubes are not internally striated (smooth walled) but are straight, and similar in diameter to brachiopod seta. They are associated with inward pointing cones (inflection) and external deflection of the shell which are also reported in *Mickwitzia* sp. from Australia (Skovsted et al. 2009). The tubes of *M. muralensis* would only represent the distal portions of outer epithelial setal follicles, that might explain the absence of casts of microvilli on the tube walls (Balthasar 2004). The presence of inner epithelial setae (located at the shell margin) in *M. muralensis* is deduced from the radiating ridges occurring in the first-formed shell and continuing as straight costae in the mature shell. They correspond to radiating folds along the margin of the larval mantle and represent initial setal follicles oriented within the plane of the shell. In *Micrina*, orthogonal pores have been reported by Williams and Holmer (2002) on the entire surface of the shell and exhibit striations on their wall. Therefore, setigerous tubes associated with inner epithelial follicle must have been present through the entire surface of the shell which therefore differs from *Mickwitzia*. Nevertheless, these tubes are inserted between phosphate laminae constituting the shell so are not shell penetrating, thus differing from the canals of *Kerberellus*. Specimens of *Micrina* sp. from Morocco, described by Skovsted et al. (2014) also exhibit non-setigerous tubes perpendicular to the shell-surface that are constructed by rings and lacking a well-defined inner wall (Skovsted et al. 2014). They are associated with setigerous tubes horizontally inserted between successive shell layers (Skovsted et al. 2014). The orthogonal tubes of *Micrina* sp. are similar to the canals of *K. marcouensis* in the sense that they are both perpendicular to the shell surface and show no traces of setae. However, the rings and the lack of well-defined inner wall in the non-setig-

erous tubes of *Micrina* sp. preclude further comparisons with *K. marcouensis*. If the canals of the latter were built in the same manner as the non-setigerous tubes of *Micrina* sp., the internal moulds of the canals would have been more irregular and traces of the rings visible. To conclude, setigerous tubes could have been absent from *K. marcouensis* or traces of the microvilli not preserved on the tube wall; they could also be associated with outer epithelial follicles. The through-going canals of *K. marcouensis*, orthogonal to the shell and present on its entire surface, might correspond to the similarly organised non-setigerous tubes of *S. significans* described by Skovsted and Holmer (2003) and Skovsted et al. (2010).

The posterior triangular-extension of the internal mould of the ventral interarea is interpreted as the infill of a median triangular sinus bisecting the ventral interarea of the original shell. The underlining, subapical, triangular depression seen in internal moulds of some valves, sometimes associated with the triangular extension, also favours interpretation of a posterior, subapical inner-fold of the shell (Fig. 4B₂, B₃). Similar structures are known from the orthocline pseudointerarea of lingulid brachiopods, functioning as a pedicle-groove, differing from the catacline subapical area of *Kerberellus*. In the paterinids, the catacline to hypercline interarea of the ventral valve is similar to the interarea of *Kerberellus*. However, it consists of a pair of flattened triangular areas (propareas) marked off from the posterolateral regions of the valve by a break in slope and separated by the delthyrium partly covered by a homeodeltidium. The configuration of the interarea of paterinids differs to that *K. marcouensis* by the protruding homeodeltidium, which would be preserved as protruding triangular ridge (buttress) on the internal mould. A subapical sinus is also present in discinoids and acrotretoids, however leading to a foramen which is absent in *Kerberellus*.

In the Mickwitziidae, the shell is supposed to have been organophosphatic but generally, it is lightly phosphatised and exhibits some acid-dissolved calcareous parts (Skovsted and Holmer 2003) or even calcareous areas visible in thin sections (possibly of diagenetic origin; Balthasar 2004). The presence of both phosphate and carbonate may correspond to the secretion of both biominerals by mickwitziids; or calcareous zones correspond to remineralised portions of originally organic material (Skovsted and Holmer 2003). *Kerberellus* may be similarly interpreted. Moreover, the shell structure differs greatly among Mickwitziidae. In *M. muralensis*, it corresponds to an alternation of porous, organic rich layers and thin compact phosphatic layers. Such a structure does not have immediate counterpart in other brachiopods but is grossly similar to that of paterinid brachiopods (Balthasar 2004). In *Setatella significans*, the shell consists of a massive outermost first-formed shell layer underlined by secondary laminated phosphatic layer pierced by vertical cylindrical structures similar to that of acrotretoid brachiopods (Skovsted and Holmer 2003). In *Mickwitzia multipunctata* McMennamin, 1992 the phosphatic shell would be organised into three layers (McMenamin 1992). Despite the wide variety of shell structures, all *Mickwitzia* display penetrating canals running through the

entire shell thickness. The Mickwitziidae also exhibit a differentiated lingulid-like juvenile (“larval”) shell that is not recognised in the described material of *Kerberellus*.

Although *Kerberellus* differs from the mickwitziids by various morphological traits, it is better interpreted as relative or member of mickwitziid-like stem-group brachiopods rather than being formally assigned to the family Mickwitziidae. The diagnosis of the family Mickwitziidae has been emended by Skovsted and Holmer (2003) and Balthasar (2004). According to these authors, the different mickwitziid species are differentiated by their shell structure, pseudointerarea, setigerous tubes, which correspond to differences in their soft part organisation. However, they included so exhaustive description of such character in the family diagnosis that only some of all the included genera and species fit. Pending further detailed phylogenetic study, it is preferable to recognise an informal group of mickwitziid-like stem-group brachiopods (Skovsted and Holmer 2003; Skovsted et al. 2010), and an exhaustive systematic revision of the mickwitziids is out of the scope of this paper.

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