FORAMINIFERAL SHELL STRUCTURES: ADDITIONAL CAVITY SYSTEMS PRODUCED BY SUPPLEMENTAL SKELETONS

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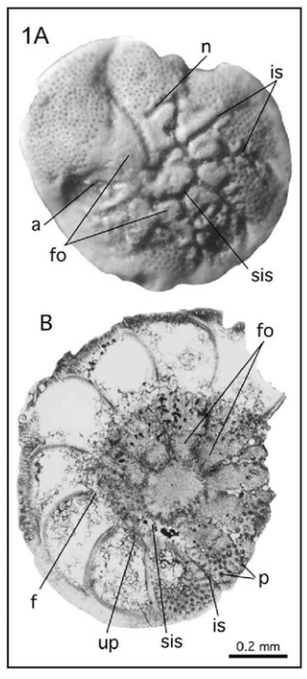
INTERLOCULAR SPACES

In bilamellar foraminiferal shells, the chamber sutures may be deeply sunken to the vicinity of an interiormarginal intercameral foramen. Thus, an interlocular space is formed between the frontal wall of the penultimate and the proximal wall of the ultimate chamber. In many comparatively simple rotaliids, the interlocular space opens on the ventral side of the test and is closed on the dorsal side. The ventral opening may be feathered, i.e. ornamented by series of grooves perpendicular to the slit produced by the sunken chamber suture (1). The interlocular space is outer space infolded into the shell and receives, therefore, secondary lamellae as far as space permits.

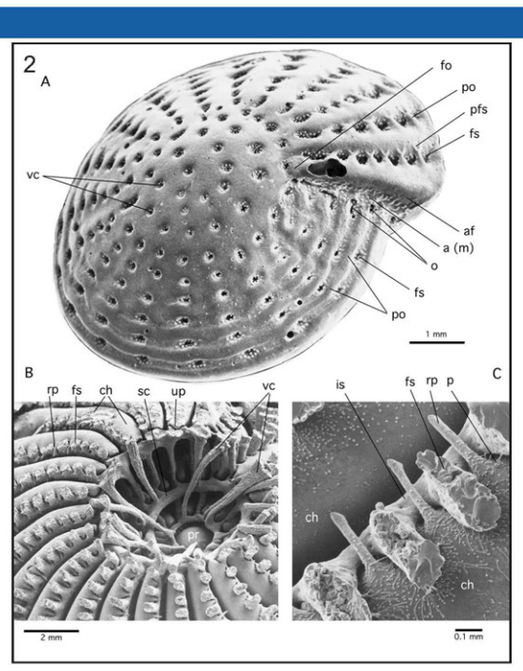


1. *Rotorbinella* sp. Late Paleocene (SBZ24), Aquitaine, France. A: external, ventral view showing feathered ventral sutures producing a shallow interlocular space. B: tangential section perpendicular to coiling axis, transmitted light.

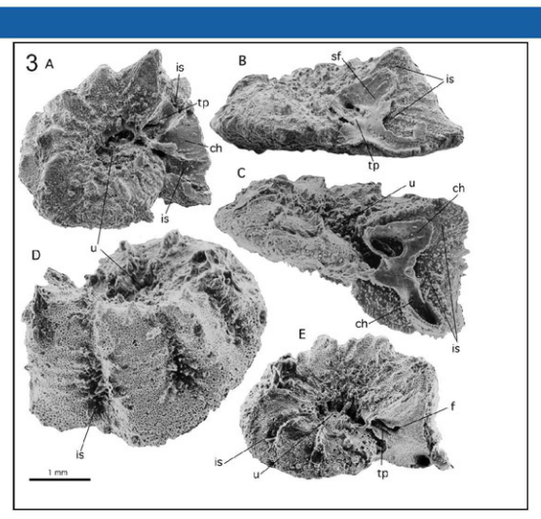
Abbreviations
a: aperture; **af**: apertural face; **alp**: alar prolongation; **a (m):** aperture (masked); **ch**: camber lumen; **co**: canal orifice; **cp**: cover plate; **env**: enveloping canals (parallel or tangential) to primary chamber wall surface; **f**: foramen; **fo**: folium; **foa**: foliar aperture; **fp**: foramenal plate; **fs**: fossette; **il**: inner lamella (= inner lining); **ils**: interlocular (intraseptal) space; **is**: (any) interlocular space; **lch**: lateral chamberlet lumen; **lat**: lateral (perforate) chamber wall; **lh**: loophole; **li**: lip (serrated); **mc**: marginal cord; **mcr**: marginal crest; **n**: notch (representing in part the plate suture); **o**: orifice (any functional opening towards the exterior); **o (c):** orifice (of canal); **p:** pore; **persk**: peripheral supplemental skeleton; **pfs**: parafossette; **pil**: pile; **po**: ponticulus; **pr**: proloculus; **psp**: pseudospine; **rc**: radial canal; **rc (sp):** radial canal in canaliferous spine; **s**: septum; **sa**: supplementary aperture; **sc**: sutural canal; **sf**: septal flap; **sis**: spiral interlocular space; **sk**: supplemental skeleton; **spc**: spiral canal; **ssc**: subsutural canal; **st**: stolon; **sulc**: sulcus; **sut**: suture; **tp**: "tooth"-plate; **u**: umbilicus; **uis**: umbilical interlocular space; **up**: umbilical plate; **vc**: vertical (umbilical) canal.

CANAL SYSTEM

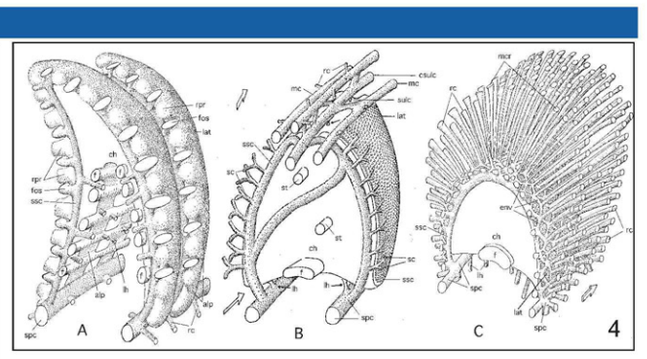
Interlocular spaces may be subdivided by retral folds of the proximal chamber wall (retral process of elphidiids) (2) or by ornamental features produced by secondary lamellation (grooves and ridges in *Miscellanea*, *Cuvillierina*, etc.) (3). The subdivided interlocular space is transformed by strictly localised resorption into (always tubular) canal systems. These communicate with umbilical spaces and cavities in manifold, diagnostic ways. The chamber cavities communicate with the canal system by small, particular openings called loopholes. These are often plugged by organic material and consequently have only temporary functions (4).



2. *Elphidium craticulatum* (Fichtel and Moll). Recent, Gulf of Aqaba, Red Sea, SEM photos. A: oblique frontal view showing masked apertures. B: epoxy resin cast of shell cavity, oblique umbilical view. C: shell cavity cast, detail showing retral processes.



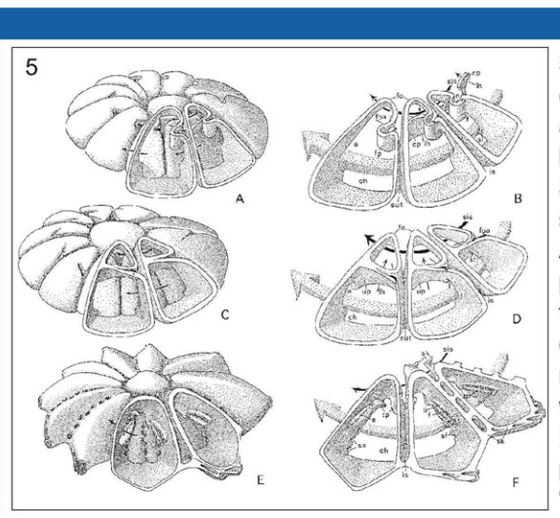
3. *Civrieuxia bicarinata* (Colom). Early Eocene, GAN, Aquitaine, France, SEM photos. A: oblique umbilical view. B, C: peripheral views. Note intraseptal space opening between the two carinae; compare with D. D: aboral, oblique peripheral view. E: oblique apertural view showing intercameral foramen with "toothplate".



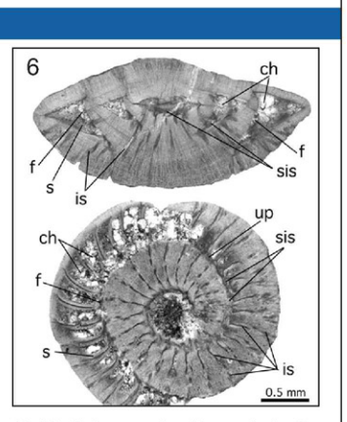
4. Chamber cavities and canal systems. Schematic, not to scale.
A: elphidiid pattern with retral processes subdividing the interlocular space.
B: operculinid pattern with marginal cord.
C: pellatispirine pattern with marginal crest.
White arrows: direction of growth.

Umbilical cavity system

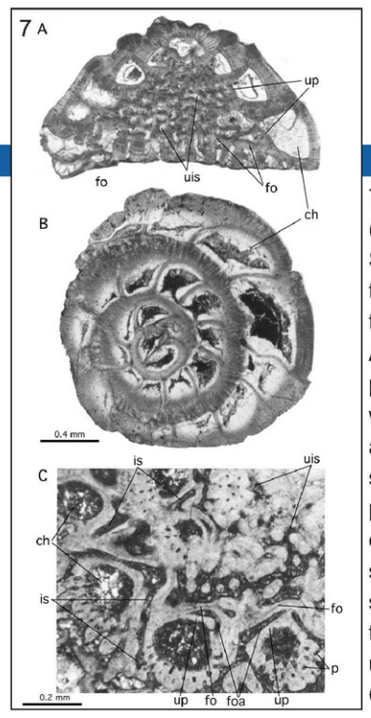
The whorl sutures in trochospiral or planispiral foraminifera exhibiting an umbilicus may also admit interlocular spaces separated from the chamber lumen by various plates attached to the primary apertures and to the previous whorl of primary chambers (5). Umbilical fills by secondary lamellation (umbilical plugs or piles) may restrict the umbilical space to a narrow spiral canal and exhibit additional, vertical umbilical canals (*Kathina*, *Dictyokathina*) (6) or umbilical cavities (*Lockhartia*) (7). The latter are generated by an umbilical extension of the ventral chamber wall, the so-called folium.



5. Separation of chamber lumen and umbilical cavity by various plates. Schematic, not to scale.
A, B: ammoniine pattern with foraminal and cover plates. C, D: rotaliine patterns with umbilical plate. E, F: pararotaliine pattern with "toothplates".



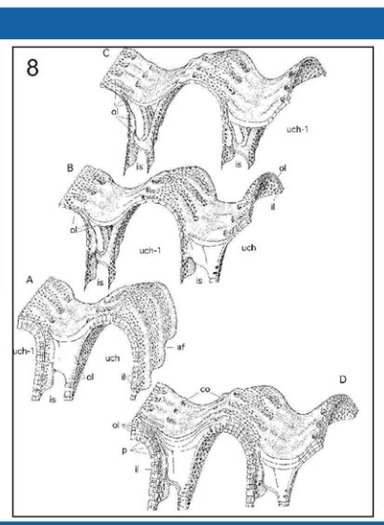
6. *Kathina major* Smout. Late Paleocene, Qatar, Persian Gulf, transmitted light. Axial section and section perpendicular to coiling axis.



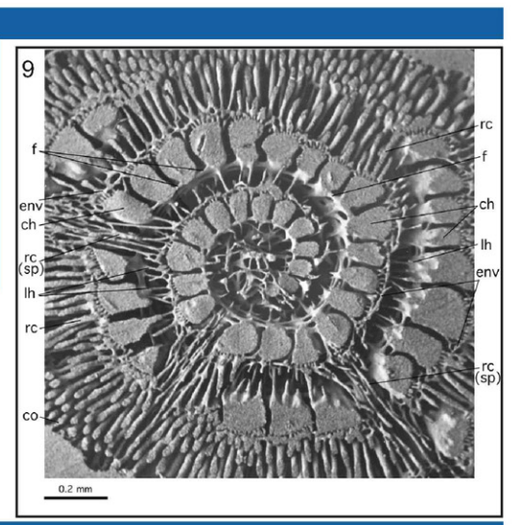
7. *Lockhartia haimei* (Davies). Paleocene, Salt Range, Pakistan, thin section in transmitted light. A: axial section, note prolongation of foliar wall up to the coiling axis of the shell. B: section approximately perpendicular to the coiling axis, showing spiral chambers. D: section perpendicular to coiling axis in umbilicus, detail. Compare 5D.

Enveloping canal system

Secondary lamellae may produce, by complex autonomous folding, series of funnels subdividing the interlocular space. Subsequent lamellae extend the funnel over the primary perforated lateral chamber wall (8).
The latter may be totally covered by a network of anastomosing canals, a so-called enveloping canal system. The walls enclosing the enveloping canal system consist exclusivelay of secondary lamellae folded upon themselves and are called supplemental skeleton. *Siderolites* and *Calcarina* represent this type of



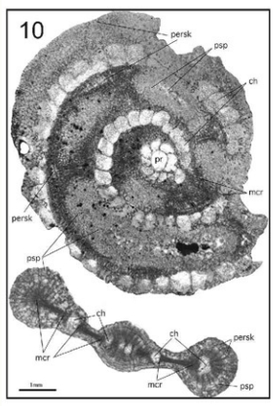
8. Formation of enveloping canal systems in *Calcarina* by successively folded outer lamellae (A-C) filling the interseptal space and growing step by step over the perforate primary bilamellar chamber wall. uch: ultimate chamber; uch-1: penultimate chamber. In D, the outer lamellae A-C are in place.



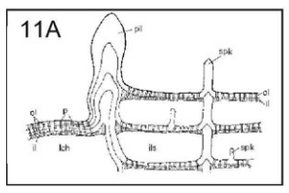
9. *Calcarina gaudichaudii* d'Orbigny. Recent, Philippines, epoxy resin cast of shell cavities, SEM photo. Section perpendicular to coiling axis.

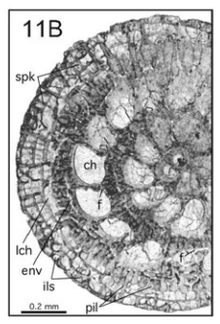
Interlamellar cavity system

Pellatispirines produce enveloping canal systems with huge radial extensions over the periphery of the planispiral test (10). These are called marginal crest (4A) (in contrast to the nummulitid marginal cord with superposed layers of tangentially directed canals; 4B).
The marginal crest may be overgrown by bilamellar perforate flying covers, suspended on ornamental spikes and pseudospines covering the previous outer surface of the shell (11). These covers produce cavities communicating with the chamber protoplast by the canal system. The cavities are called here interlamellar because they seem to be generated by low interlamellar gaps in the supplemental skeleton. However, they are produced by a primary bilamellar and perforated wall, may substitute regular chambers and support in their turn secondary, perforate lamellation, as seen in *Vacuolispira* (12). The cavities overgrowing extended marginal crest may be inflated to form more or less irregular lateral chamberlets, as in *Biplanispira* (13), but lack direct connections with the main chamber cavities through a stolon system, as in *Orbitoides*. The walls delimiting interlamellar cavities are difficult to separate from the underlying supplemental skeleton and are, therefore, included into its definition (14).

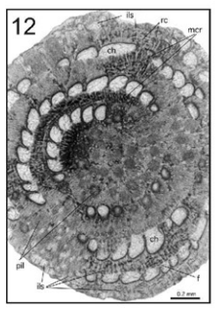


10. *Pellatispira fulgeria* Whipple. Late Eocene, Kalimantan, Indonesia (Borneo), transmitted light. Equatorial and axial thin section. Note the excessively broad marginal crest.

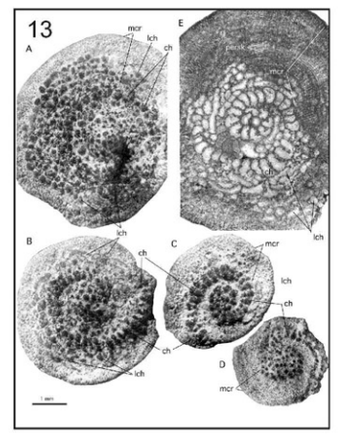




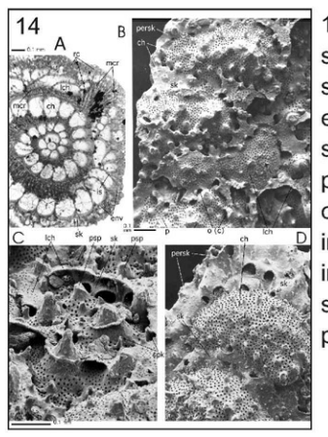
11. Flying covers of perforated (bilamellar) wall suspended on spikes and piles.
A: lamellar disposition, schematic, not to scale.
B: *Vacuolispira inflata* (Umbgrove). Late Eocene, Kalimantan, Indonesia (Borneo), transmitted light. Approximately equatorial thin section. Note ultimate growth stage covered by interlamellar cavities (brood chambers?).



12. *Vacuolispira irregularis* (Umbgrove). Late Eocene, Kalimantan, Indonesia (Borneo), transmitted light. Non-centered oblique thin section near equatorial plane. Note incipient interlamellar cavities in the walls adjacent to the marginal crest.



13. Lateral chamberlets formed by inflation of interlamellar cavities in *Biplanispira absurda* Umbgrove, Late Eocene, Igualada, Spain.
A-D: external, lateral views of growth series showing successive overgrowth of marginal crest. E: slightly oblique, equatorial section tangential to proloculus, seen in transmitted light.



14. Elements of supplemental skeleton in early growth stages of pellatispirines, covering intraseptal interlocular space and periphery.

A-D: *Pellatispira* aff. *provalei* Yabe. Empty shells from Kalimantan, Indonesia (Borneo), Late Eocene. A: equatorial thin section, transmitted light. B: lateral view of shell, marginal crest broken, SEM photo. C: oblique, lateral view, perforate walls of lateral chamberlets broken in order to show the suspension of the walls on spikes and piles. D: lateral view of shell, detail showing imperforated walls of marginal crest and perforated walls of spiral chambers.