

MORPHOLOGY OF ENCRUSTING AND FREE LIVING ACERVULINID FORAMINIFERA: *ACERVULINA, GYPSINA AND SOLENUMERIS*

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ABSTRACT. The generic identification of acervulinids is especially difficult due to a confused systematics. However, this family is of major interest because it comprises the main encrusting reef Foraminifera which can contribute significantly to the reef framework or build true reefs up to several kilometres in length. Their close dependency on the substratum to which they are attached and their ability to develop various growth forms result in an irregular morphology and arrangement of the chambers. This has certainly contributed to the difficulty of defining accurate criteria for identification of genera and species. Moreover, the ability of the Eocene acervulinid *Solenomeris* to build monospecific, kilometre-sized reefs has misled most previous workers to consider it as a red alga. The geometrical characteristics of the test of the main acervulinid genera (*Acervulina*, *Borodinia*, *Gypsina*, *Solenomeris*) are analysed and discussed, based on previous descriptions and personal observations. This leads to some reliable and easily usable criteria for genera and species identification. *Solenomeris* is very close to *Acervulina* but can be distinguished by the form of the juvenile.

THE Acervulinidae includes sessile Foraminifera, often with an encrusting growth form, which are able to contribute significantly to the reef framework or even to build true monospecific reef biostromes (Plaziat 1984; Perrin 1987a, 1987b, 1987c, 1989, 1992; Plaziat and Perrin 1992) and consequently is of major interest for palaeoenvironmental interpretation of Recent and Tertiary reef facies. Like all attached organisms, acervulinids closely depend on the substratum they encrust; the irregularities of the substratum surface influence the internal organization of the crust. Moreover, like other reef-building organisms (e.g. scleractinians and Rhodophyceae), acervulinids have developed various growth forms according to different environmental conditions (Perrin 1989, 1992).

The direct influence of the substratum on acervulinids and their tendency to develop different growth forms are reflected in the irregularity of the geometry and arrangement of chambers. This irregularity of the internal organization of the skeleton is probably one of the main causes of the especially confused systematics of this family and has certainly contributed to the difficulty of finding accurate criteria for the identification of genera and species. In particular, criteria for the distinction between *Acervulina* and *Gypsina* have never been clearly defined. Moreover, the ability of the Eocene *Solenomeris* to build monospecific, kilometre-sized reefs has led most previous authors to consider them as red algae.

The most frequently quoted genera in reef environments are the fossil genus *Solenomeris*, and the fossil to Recent genera *Acervulina* and *Gypsina*. This paper aims to provide reliable criteria for generic and specific identification of acervulinids.

THE ACERVULINIDAE

Previous systematic studies of the family

The Acervulinidae was created by Schultze (1854) for *Acervulina* Schultze, 1854 (type species *A. inhaerens* Schultze, 1854). This author also described two other species of the genus (*A. globosa* and *A. acinosa*) which do not seem to have been reported by subsequent authors, probably because of

their very brief description and inadequate figures which show only the external appearance of the test. *Gypsina* was described by Carter (1877) on the basis of a specimen described by Carpenter (1876) and named *Tinoporus vesicularis*, itself a synonym of *Orbitolina vesicularis*. This last species created by Parker and Jones (1860) therefore corresponds to the type species of *Gypsina*. Carter (1877) also reported another species, *Gypsina melobesioides*, which he considered a synonym of *Polytrema planum* previously created by himself (Carter 1876). This has resulted in much confusion concerning both *Acervulina* and *Gypsina*. With the creation of *Gypsina*, Schultze's work (1854) concerning *Acervulina* became neglected and most of the subsequently described species were placed in *Gypsina* and often in the Planorbulinidae. Brady (1884) referred Schultze's species *A. inhaerens* to *Gypsina* without explanation. The type species of *Acervulina* was first designated by Galloway and Wissler (1927), and that of *Gypsina* by Cushman (1915). However, some authors have considered *Gypsina melobesioides* and consequently *Polytrema planum* as the type species of *Gypsina* (Loeblich and Tappan 1964; Moussavian 1989), though this species, sometimes named *Gypsina plana* (Cushman *et al.* 1954), is considered by most authors as a synonym of *Acervulina inhaerens* Schultze, 1854 (see Galloway and Wissler 1927) or its variety *plana* Hanzawa, 1931 (see Hanzawa 1931, 1957). Galloway and Wissler (1927) and Moussavian (1989) therefore regarded *Acervulina* and *Gypsina* as synonyms since *Polytrema planum*, which they considered as the type species of *Gypsina*, is an *Acervulina*.

Among the various subsequently described genera placed in this family some, like the unilocular form *Semseya* Franzenau, 1893 (monotypic type species *Semseya lamellata*), *Pseudogypsina* Trauth, 1918 (monotypic type species *Pseudogypsina multiformis*) and *Borodinia* Hanzawa, 1940 (monotypic type species *Borodinia septentrionalis*), remain extremely rare or very little known. Other genera were created from existing species or varieties of *Gypsina*: *Sphaerogypsina* Galloway, 1933 (type species *Gypsina globulus* Reuss, 1848), *Discogypsina* Silvestri, 1937 (type species *Gypsina vesicularis* var. *discus* Goës, 1882), *Planogypsina* Bermudez, 1952 (type species *Gypsina mastelensis* Bursch, 1947). *Ladoronia*, created by Hanzawa (1957) as a subgenus of *Acervulina* (type species *Acervulina (Ladoronia) vermicularis* Hanzawa, 1957), was considered as a genus by Loeblich and Tappan (1964).

Douvillé (1924) independently created the genus *Solenomeris* (type species *Solenomeris O'Gormani* [sic]) from an Eocene encrusting organism he identified as a red alga and which corresponds to the Austrian Eocene form described by Trauth (1918) as *Polytrema planum* (= *Acervulina inhaerens* var. *plana*). Other species belonging to the same genus were described mainly as red algae (as Solenoporacea or more rarely as coralline algae): *S. douvillei* Pfender, 1926, *S. afonensis* Maslov, 1956 and *S. pakistense* Johnson and Konishi, 1960. However, several authors have placed *Solenomeris* in the Acervulinidae (Hagn and Wellnhofer 1967; Hagn 1967, 1978, 1983; Moussavian 1984, 1989; Perrin 1987a, 1987b, 1987c, 1992; Plaziat and Perrin 1992), some of them considering it as a synonym of *Gypsina* (Hagn 1972, 1978, 1983; Moussavian 1984) or *Acervulina* (Moussavian 1989).

Identification of the Acervulinidae

The test of Acervulinidae consists of hyaline calcite and the walls are formed like those of the other Rotaliina, by two calcified layers on both sides of an organic membrane (Hansen and Reiss 1971). The test may be free or attached to a substratum (Schultze 1854; Galloway 1933; Loeblich and Tappan 1964). Acervulinid growth is characterized by a spiral coiling of the early chambers, followed by adult chambers arranged in one or several layers, without any apertures other than wall pores, and without a canal system (Schultze 1854; Cushman 1950; Loeblich and Tappan 1964, 1984). However, there are some other characters common to the different genera of Acervulinidae, especially the typical arrangement of the adult chambers alternating from one layer to the next in multilayered tests.

Loeblich and Tappan (1964, 1984) suggested a stratigraphical range for this family from Eocene to Recent. However, Cushman (1950) reported some acervulinids (*Acervulina* and *Gypsina*)

TEXT-FIG. 1. Arrangement of chambers in subaxial section (left) and in transverse section (right) in species of *Acervulina*. A, *A. inhaerens*; B, *A. linearis*; C, *A. (Ladoronia) vermicularis*; $\times 56$.

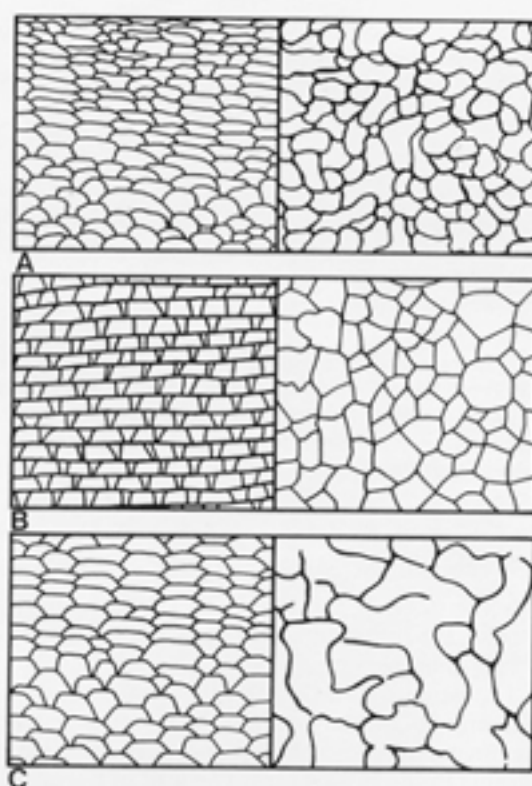


TABLE 1. Size of main features of the test of *Acervulina inhaerens* Schultze, 1854.

References and localities ...		<i>G. inhaerens</i> Yabe and Hanzawa 1925 Ryukyu Id. Taiwan	<i>var. plana</i> Hanzawa 1931 Japan	<i>var. plana</i> Hanzawa 1957 Micronesia			
Test							
Diameter (mm)		—	—	—	—	—	—
Thickness (mm)		—	—	—	—	—	—
Juvenile stages							
Proloculus	Diameter (μm)	—	—	—	—	—	—
Equatorial chambers	Width (μm)	—	—	—	—	—	—
	Height (μm)	—	—	—	—	—	—
Adult stage							
Lateral chambers	Width (μm)	70–230	74–140	70–90	50–230	56–100	56–130
	Height (μm)	—	32–43	—	5	18–47	23
Tangential wall	Thickness (μm)	5	—	5	5	5	5
Lateral wall	Thickness (μm)	5	—	5	5	5	5
Pores	Diameter (μm)	5–7	—	5	5	5	5
Stolons	Diameter (μm)	—	—	—	—	—	—

from the Cretaceous. Moreover, specimens of *Acervulina* from the Upper Jurassic of Central Japan have been described by Hanzawa (1939).

PRINCIPAL GENERA OF ACERVULINIDAE

Acervulina

Stratigraphical range. *Acervulina* is mainly reported from Cenozoic to Recent (Loeblich and Tappan 1964). However, it is considered to have appeared before the end of the Mesozoic (Cushman 1950). Moreover, Hanzawa (1939) described a variety of *Acervulina inhaerens* var. *huzimotoi* from an Upper Jurassic bioclastic limestone in central Japan.

Type species. The type species *Acervulina inhaerens* (Text-fig. 1; Table 1), was described by Schultze (1854) from a Recent shallow water specimen from the Ancona region of Italy. According to Schultze, it is characterized by an attached or free-living test made up of a small number of chambers, each having a diameter of 60 μm . The shell has a hyaline structure and is perforated by pores of 1 to 15 μm diameter. The material studied here comes from Plio-Quaternary reefal limestone of Mururoa Atoll (French Polynesia).

Acervulina inhaerens

Juvenile stages (Pl. 1, figs 1–2). The growth of juvenile forms can be divided into two main stages (Perrin 1987a): coiling development of the equatorial layer (or equatorial disc); and addition of lateral chambers.

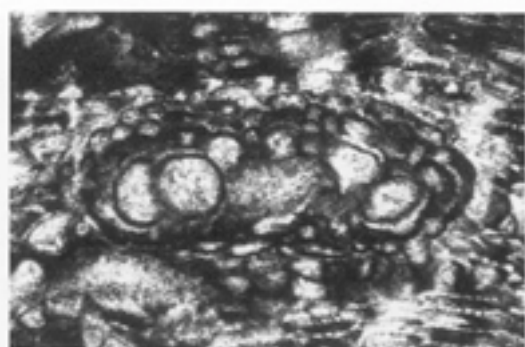
The equatorial layer (or equatorial disc) consists of spherical or subspherical chambers (average diameter 80 μm) larger than the lateral chambers and formed in a planospiral arrangement around the proloculus and the second peri-embryonary chamber. This equatorial disc is approximately parallel to the substratum. The wall of the equatorial chambers appears imperforate but shows, like the adult chambers, a dark median line separating two layers of fibrous hyaline calcite.

The lateral chambers present the same characteristics (shape and size) as the adult chambers. They are arranged in successive layers around the equatorial disc, chambers alternating from one layer to the next. In axial section, the three or four earlier successive layers of lateral chambers form a slightly compressed oval (about 600 μm long and 200 μm high) showing a free bipolar growth. Thus these earlier layers of lateral chambers intercalate between the equatorial layer and the substratum. This indicates that their formation occurred before any attachment of the organism to the substratum. Therefore, during this growth stage the organism was free-living and became attached to a substratum only after the constitution of the third or fourth layer of lateral chambers.

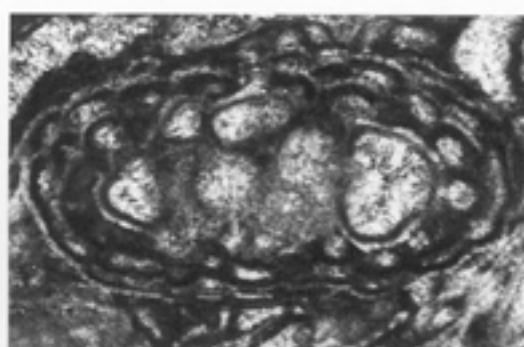
EXPLANATION OF PLATE I

Figs 1–8. *Acervulina inhaerens* Schultze, 1854. Mururoa atoll, Plio-Quaternary. 1, subaxial thin section showing the ovoid of the juvenile stages; UPS Orsay F146; $\times 85$. 2, ovoid of the juvenile stages in subaxial thin section; UPS Orsay F146; $\times 125$. 3, arrangement of adult chambers in axial ultrathin section showing the pores within the chamber roofs and some stolons in the lateral walls; UPS Orsay Ac4; $\times 160$. 4, SEM of axial section of adult chambers; the chamber roofs and floors are perforated and consist of two layers of fibrous calcite developed on both sides of a median line; UPS Orsay Ac4'; $\times 490$. 5, SEM showing the pores in the chambers roofs and floors; the median line of the chamber wall is continuous through the pores; UPS Orsay Ac7'; $\times 330$. 6, SEM of tangential section through the chamber roofs showing the pores; UPS Orsay Ac8'; $\times 175$. 7, adult chambers in tangential ultrathin section showing the microstructure of the chamber walls; the hyaline fibrous calcite of the chamber walls appears darker than the high-magnesian calcitic cement filling the internal part of the chambers; UPS Orsay Ac1; $\times 160$. 8, SEM of oblique section showing the pores through the tangential walls; UPS Orsay Ac7'; $\times 270$.

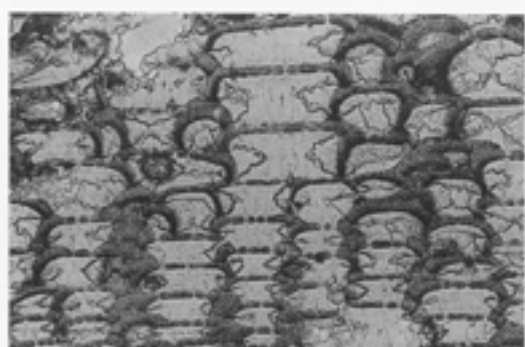
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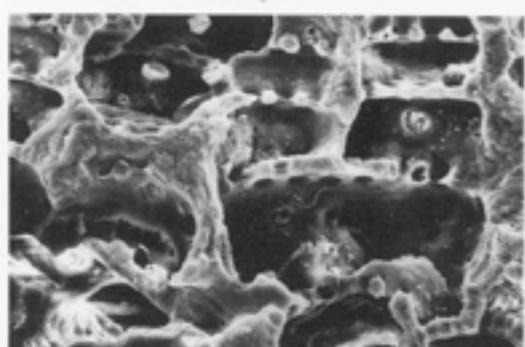
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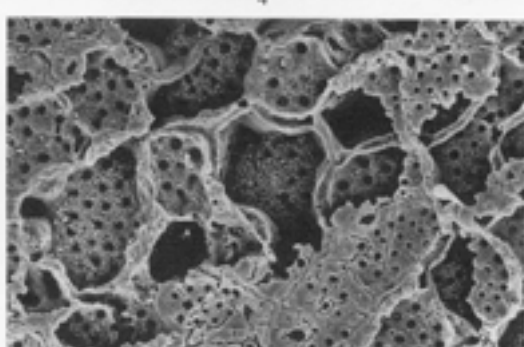
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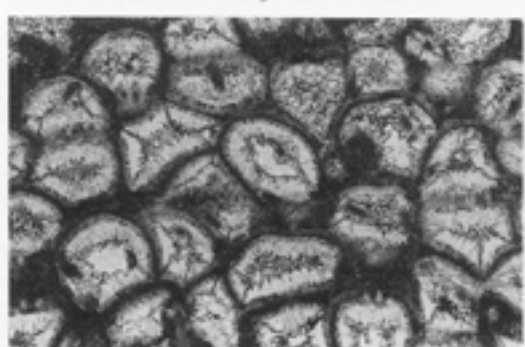
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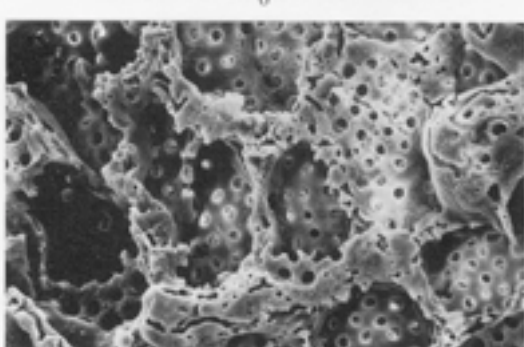
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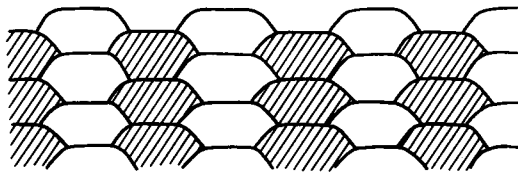


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Adult stage. Contrary to the juvenile stages, the adult stage is characterized by a unipolar encrusting growth. The juvenile settled on a rigid substratum and began to encrust it, adding successive layers of chambers above and around the compressed ovoid. The thin crust followed the irregularities of the substratum and, consequently, the arrangement of chambers is often irregular.

According to Hanzawa (1947, 1957), *Acervulina inhaerens* (Text-fig. 1; Table 1) is characterized by upwardly arched roofs in axial section. However, in axial section, the adult chambers of the Mururoa specimens have a flattened subhexagonal shape and are arranged one above the other in successive layers with chambers alternating from one layer to the next (Pl. 1, figs 3–4). Chamber height is about 25–30 μm , while their average width is 70 μm .

Each hexagonal chamber of a layer 'n' is delimited at its base by the roof of the underlying chamber (layer 'n-2') and the lateral walls of the two chambers of the preceding layer ('n-1'). Its upper part is delimited by the roof and lateral walls, both newly formed, the lateral walls resting on the lower lateral walls or, more rarely, on the roofs of the two chambers of the preceding layer (Pl. 1, fig. 5; Text-fig. 2).



TEXT-FIG. 2. Adult stage of *Acervulina* showing the formation of vertical stacks from the successive layers of chambers; $\times 150$.

In tangential section, the adult chambers have a rounded and irregular shape. Their diameter is c. 60–80 μm . The shape and arrangement of the chambers is often more or less irregular due to changes of growth direction during the development of the crust.

The chamber walls show the typical wall structure of lamellar hyaline Foraminifera (Hansen and Reiss 1971; Haynes 1981; Loeblich and Tappan 1984): two layers of fibrous hyaline calcite are developed on both sides of a dark median layer (Pl. 1, fig. 4).

The flattened part of the wall forming the roof or floor of chambers or tangential wall is coarsely perforated, the pores being 5–7 μm in diameter (Pl. 1, figs 6, 8). In ultrathin sections and in scanning electron microscopy, the dark median layer of the tangential walls of Recent *Acervulina* appears to be continuous through the pores (Pl. 1, figs 4–5, 7).

The lateral walls show the same bilamellar structure bending downwards from the roof of the chamber and leaning against the walls of the chambers of the underlying layer. However, the lateral walls are imperforate.

The occurrence of stolons connecting adjacent chambers of the same layer has been reported by Hanzawa (1957) but with some reservations, and later by Reiss and Hottinger (1984). Stolons emerging from the lateral walls of adult chambers have been clearly observed in ultrathin sections and in scanning electron micrographs of specimens from the cored wells of Mururoa Atoll (Pl. 1, fig. 3).

The variety *plana* is separated according to the larger size of its chambers (Yabe and Hanzawa 1925; Hanzawa 1931). On the other hand, the Jurassic variety *huzimotoi* (Hanzawa 1939) shows smaller chambers and is also differentiated by its exceptionally thick sinuous walls (12–16 μm) visible in tangential sections (Hanzawa 1939).

Other species

According to Hanzawa (1947, 1957), *Acervulina* is represented by two other encrusting species: *Acervulina (Acervulina) linearis* Hanzawa, 1947; and *Acervulina (Ladoronia) vermicularis* Hanzawa, 1957. *Acervulina linearis* (Text-fig. 1; Table 2) was first described by Hanzawa (1947) from the Eocene of Micronesia and differs from the type species by its non-arched roofs. The roofs of the adjacent flat chambers constitute a straight line in axial section. The lateral walls are perpendicular or slightly oblique to the roof plane and do not show any stolons (Hanzawa 1947, 1957). The subgenus *Ladoronia* created by Hanzawa (1957) is based on *Acervulina*

TABLE 2. Size of main features of the test of *Acervulina linearis* Hanzawa, 1947.

References and localities...		<i>A. linearis</i> Hanzawa 1947		<i>A. linearis</i> Hanzawa 1957	<i>A. linearis</i> Hagn and Wellnhofer 1967
		New Britain	Marshall Id.	Micronesia	Alps (Pfaffing)
Test					
Diameter (mm)		—	—	—	10 max.
Thickness (mm)		—	—	—	—
Juvenile stages					
Proloculus	Diameter (μm)	—	—	—	—
Equatorial chambers	Width (μm)	—	—	—	—
	Height (μm)	—	—	—	—
Adult stage					
Lateral chambers	Width (μm)	15–50	37–62	37–62 (211 max.)	—
	Height (μm)	15–50	11–30	11–30	—
Tangential wall	Thickness (μm)	5	5	5	4.5–9
Lateral wall	Thickness (μm)	5	5	5	4.5–9
Pores	Diameter (μm)	5–10	5–11	5–11	5
Stolons	Diameter (μm)	—	—	—	—

(*Ladoronia*) *vermicularis* from an Upper Oligocene–Aquitainian limestone of Micronesia (Text-fig. 1; Table 3). This species possesses chambers larger than *Acervulina inhaerens* and characterized by their elongated sinuous shape in tangential section. These chambers communicate by way of stolons within the same layer (Hanzawa 1957). The juvenile stages of this species have been described by Hanzawa (1957, pp. 68–69) as a ‘raspberry-like embryonic apparatus’ encircled by ‘two or three annuli of arcuate chambers’. The nepionic chambers show thick roofs ($> 100 \mu\text{m}$) within which vertical nontubulous pillars are embedded. The neanic chambers are large and vermicular-shaped and have thick vertical lateral walls pierced by large stolons (Hanzawa 1957).

Generic characteristics of *Acervulina*

The juvenile stages of *Acervulina* are free and characterized by the formation of a three-layered ovoid. The equatorial layer consists of a planospiral arrangement of subspherical large chambers around the proloculus and the second periembrionar chamber. This first stage is followed by the addition of layers of lateral chambers on each side of the equatorial disc, forming the ventral and dorsal zones.

The adult stage is attached to a substratum by the ventral face and is characterized by a unipolar growth of the dorsal zone. The adult chambers are subhexagonal in axial section and show rounded shapes in tangential section. They are arranged in successive layers with chambers alternating from one layer to the next one. Tangential and lateral walls show a thickness of a few microns (5–7 μm). Chambers from successive layers communicate by way of perforations of the roofs (tangential walls) of the chambers.

The distinction of the three species of *Acervulina* appears to be mainly based on the size and the shape of chambers (Text-fig. 1).

Growth pattern

The genus *Acervulina* includes encrusting forms with very different thicknesses: from less than one millimetre to several centimetres. *Acervulina* (*Ladoronia*) *vermicularis* generally forms a thin crust (Hanzawa 1957), whereas *Acervulina inhaerens* constitutes millimetre-thick as well as decimetre-thick crusts (Yabe and Hanzawa 1925; Galloway and Wissler 1927; Hanzawa 1939; Hottinger 1983; Reiss and Hottinger 1984; Perrin 1987b, 1989, 1990, 1992). Moreover, *A. inhaerens* can

TABLE 3. Size of main features of the test of *Acervulina (Ladoronia) vermicularis* Hanzawa, 1957.

Reference and locality...	<i>A. (Ladoronia) vermicularis</i> Hanzawa 1957 Micronesia	
Test		
Diameter (mm)		—
Thickness (mm)		—
Juvenile stages		
Proloculus	Diameter (μm)	68
Equatorial chambers	Width (μm)	—
	Height (μm)	—
Adult stage		
Lateral chambers	Width (μm)	—
	Height (μm)	—
Tangential wall	Thickness (μm)	9–24
Lateral wall	Thickness (μm)	9
Pores	Diameter (μm)	5
Stolons	Diameter (μm)	14

develop different morphologies according to environmental conditions (Hottinger 1983; Reiss and Hottinger 1984; Perrin 1989, 1992), the most frequently observed being crusts a few millimetres thick, extending over a surface area of a few square centimetres. Nodules or macroids (*sensu* Hottinger 1983) with a centimetre to decimetre diameter have been described at the base of reef-slopes (Chapman 1900; Logan *et al.* 1969; Hottinger 1983; Reiss and Hottinger 1984; Dullo *et al.* 1990). Moreover, in some cored wells of the Mururoa Atoll, *Acervulina inhaerens* is responsible for boundstones formed by decimetre-thick crusts which characterize the palaeoenvironments of deeper external reef-slopes (Perrin 1989, 1990, 1992).

Borodinia

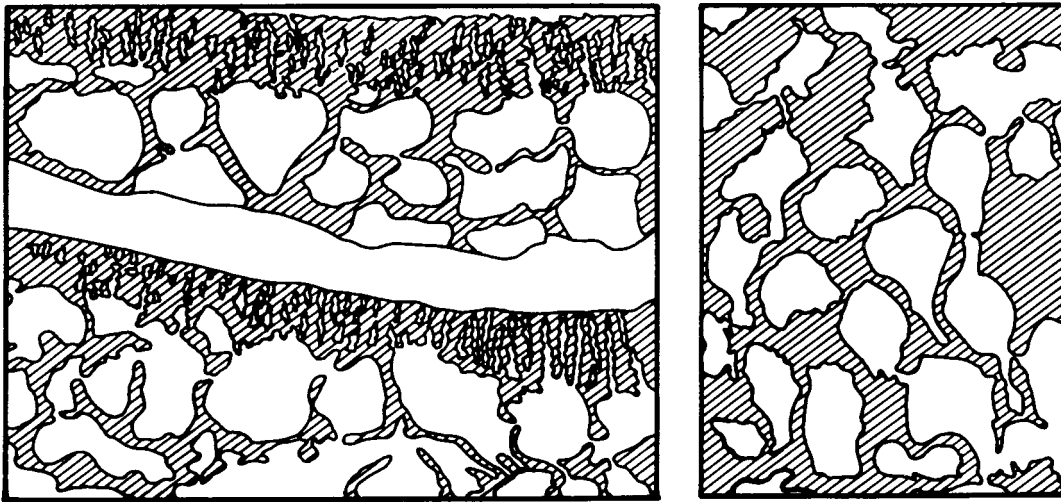
Stratigraphical range. This genus was created by Hanzawa (1940) for encrusting Foraminifera from the Aquitanian limestone of Kita Daito Jima (China Sea) and was later recorded by the same author from the Aquitanian limestones of Micronesia (Hanzawa 1957). Being very rarely reported, its stratigraphical range is especially difficult to establish.

Type species. According to Hanzawa's description of the type species, *B. septentrionalis* Hanzawa, 1940, from the Aquitanian limestone of Kita Daito Jima drill cores, this encrusting foraminifer forms a layer of one or more zones of chambers. The outer wall of the shell is 37–75 μm thick and shows coarse pores of 11 μm diameter. The chambers are irregularly arranged and each of them consists of an arched tangential wall and lateral walls of the same 12–25 μm thickness. Both lateral walls of each chamber are pierced by large stolons of 37 μm diameter.

Borodinia septentrionalis

Juvenile stages. The organization of the earlier chambers is similar to *Planorbulina* and shows a planospiral arrangement (Hanzawa 1957).

Adult stage. The adult chambers are very irregularly arranged in alternating successive layers (Hanzawa 1957; Loeblich and Tappan 1964). In transverse sections, some chambers are typically spatuliform and the adjacent chambers communicate with each other by several stolons (Text-fig. 3; Table 4). The roofs of chambers are especially thick (140 μm) in comparison with the average size



TEXT-FIG. 3. Arrangement of chambers in subaxial section (left), showing the finely cribrate roofs, and in transverse section (right), with numerous stolons, in *Borodinia* (after Hanzawa 1957); $\times 70$.

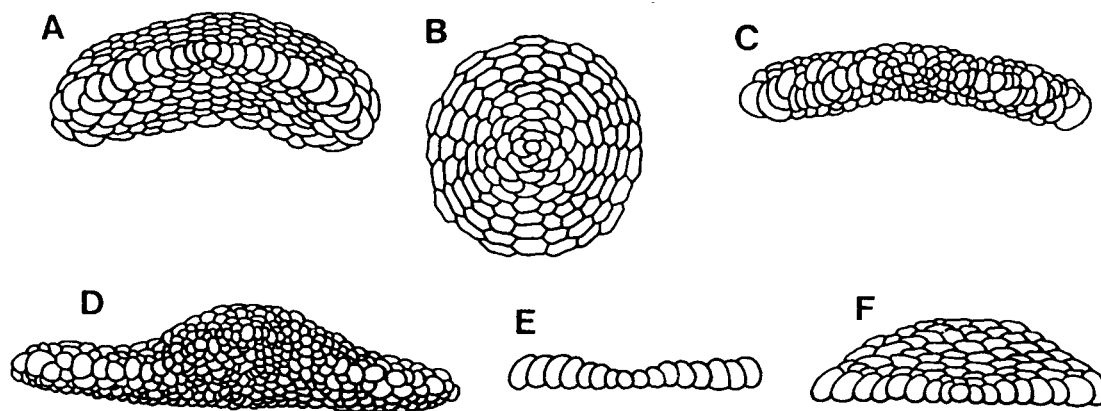
TABLE 4. Size of main features of the test of *Borodinia septentrionalis* Hanzawa, 1940 (after Hanzawa 1940, 1957).

Reference and locality...		<i>Borodinia septentrionalis</i> Hanzawa 1957 Micronesia	
Test			
Diameter (mm)		—	
Thickness (mm)		—	
Juvenile stages			
Proloculus	Diameter (μm)	—	
Equatorial chambers	Width (μm)	—	
	Height (μm)	—	
Adult stage			
Lateral chambers	Width (μm)	120–210	
	Height (μm)	122	
Tangential wall	Thickness (μm)	140	
Lateral wall	Thickness (μm)	20	
Pores	Diameter (μm)	9	
Stolons	Diameter (μm)	14	

of chambers ($100\text{--}200 \mu\text{m} \times 122 \mu\text{m}$), while the thickness of lateral walls is $20 \mu\text{m}$ (Table 4). The roof wall is finely perforated (Hanzawa 1957).

Generic characteristics of *Borodinia*

Borodinia is characterized by a planospiral arrangement in the juvenile stage. The adult chambers show a very irregular shape, often spatuliform in tangential section, and they communicate with adjacent chambers by means of stolons. Tangential walls of adult chambers have a thickness of more than $100 \mu\text{m}$ and are perforated by pore canals (Hanzawa 1940, 1957; Text-fig. 3).



TEXT-FIG. 4. Different species of *Gypsina* in vertical section. A, *G. vesicularis*; B, *G. globulus*; C, *G. saipanensis*; D, *G. marianensis*; E, *G. squamiformis*; F, *G. mastelensis*; $\times 26$.

TABLE 5. Size of main features of the test of *Gypsina vesicularis* (Parker and Jones, 1860).

References and localities...		<i>G. vesicularis</i> Bursch 1947 Mollusk Id	<i>G. vesicularis</i> Hanzawa 1957 Micronesia
Test			
Diameter (mm)		2.9 max.	1.3-1.7
Thickness (mm)		0.65	0.56-0.79
Juvenile stages			
Proloculus	Diameter (μm)	—	47-78
Equatorial chambers	Width (μm)	—	44-70
	Height (μm)	—	44-140
Adult stage			
Lateral chambers	Width (μm)	80	60-82
	Height (μm)	5-20	5-25
Tangential wall	Thickness (μm)	5-10	10-14
Lateral wall	Thickness (μm)	10-15	—
Pores	Diameter (μm)	5	5
Stolons	Diameter (μm)	—	—

Growth pattern

The specimens described by Hanzawa (1940, 1957) are encrusting forms but no indication about the extent and the thickness of the crust is given.

Gypsina

Stratigraphical range. This genus is generally reported from the Eocene to Recent (Bursch 1947; Hanzawa 1957; Loeblich and Tappan 1964), but Cushman (1950) considered it as probably dating back to the Cretaceous.

Type species. *Gypsina* was created by Carter (1877) for *Tinoporus vesicularis* Carpenter, 1876, a synonym of *Orbitolina vesicularis* Parker and Jones, 1860. The type species of *Gypsina* is therefore *Gypsina vesicularis* (Parker and Jones, 1860), from Recent coral-reef sediment of Australia.

The type-specimen described by Parker and Jones (1860) has a slightly conical test of 2.5 mm diameter consisting of vesicular chambers (tangential section), some of them showing polygonal shapes, arranged alternately concentrically (axial section). The equatorial disk, referred to as the 'primary disk', is generally covered by additional layers of chambers (dorsal lateral chambers) and the 'umbilicus is filled up so that the base of the cone is almost flat' (ventral lateral chambers). The walls have coarse pores referred as 'pseudopodial passages' (Parker and Jones 1860, pp. 31-32).

Gypsina vesicularis

This species (Text-fig. 4A; Table 5) has a discoidal test with a convex or conical shape and a thickened round periphery. The proloculus is spherical and located at the centre of the equatorial layer (Bursch 1947; Hanzawa 1957). The equatorial chambers have arched shapes and larger size than lateral chambers. They show stolons at the edges and perforations in the arched parts of their walls (Bursch 1947). The lateral chambers surround the equatorial disc and are symmetrically arranged on both sides of the median (equatorial) layer (Brady 1884; Hanzawa 1931, 1957; Bursch 1947; Cushman *et al.* 1954). They show the same shape and the same arrangement as the lateral chambers of *Acervulina*. Each chamber communicates with the adjacent chambers through stolons at the base of lateral walls, and with the chambers situated above and below through perforations in the tangential wall (Bursch 1947; Hanzawa 1957).

Gypsina discus Goës (see Bursch 1947) is now considered as a variety of the type species (Hanzawa 1957) characterized by its discoidal shape. It is the type species of *Discogypsina* Silvestri, 1937.

Other species

According to Hanzawa (1931, 1957) and Bursch (1947), *Gypsina* is represented by at least five other species: *G. globulus* (Reuss, 1848); *G. squamiformis* Chapman, 1900; *G. mastelensis* Bursch, 1947; *G. saipanensis* Hanzawa, 1957; *G. marianensis* Hanzawa, 1957.

Gypsina globulus (Text-fig. 4B; Table 6), which was first described by Reuss (1848) as *Cerriopora globulus*, is characterized by its spherical to subovoidal shape and more regular arrangement of the chambers, smaller chambers and finer pores than other *Gypsina* species. It also lacks the median layer (Brady 1884; Hanzawa 1931; Bursch 1947; Cushman *et al.* 1954). Bursch (1947) described a megalospheric *juvenarium* composed of two embryonar chambers and two auxiliary chambers. Stolons occur within the lateral walls of adult chambers

TABLE 6. Size of main features of the test of *Gypsina globulus* (Reuss, 1848).

References and localities ...		<i>G. globulus</i> Hanzawa 1931 Japan	<i>G. globulus</i> Bursch 1947 Mollusk Id.	<i>G. globulus</i> Hanzawa 1957 Micronesia
Test				
Diameter (mm)		2.25	0.5-1	1.4-2.0
Thickness (mm)		—	—	—
Juvenile stages				
Proloculus	Diameter (μ m)	—	37	—
Equatorial chambers	Width (μ m)	—	—	—
	Height (μ m)	—	—	—
Adult stage				
Lateral chambers	Width (μ m)	—	60	150-180
	Height (μ m)	—	50	25-50
Tangential wall	Thickness (μ m)	—	3-6	10-15
Lateral wall	Thickness (μ m)	—	5-8	—
Pores	Diameter (μ m)	—	5	5
Stolons	Diameter (μ m)	—	5	—

TABLE 7. Size of main features of the test of *Gypsina squamiformis* Chapman, 1900.

Reference and locality ...		<i>G. squamiformis</i> Bursch 1947 Mollusk Id
Test		
Diameter (mm)		1
Thickness (mm)		—
Juvenile stages		
Proloculus	Diameter (μm)	—
Equatorial chambers	Width (μm)	—
	Height (μm)	120
Adult stage		
Lateral chambers	Width (μm)	—
	Height (μm)	—
Tangential wall	Thickness (μm)	—
Lateral wall	Thickness (μm)	—
Pores	Diameter (μm)	4–5
Stolons	Diameter (μm)	30 max.

TABLE 8. Size of main features of the test of *Gypsina mastelensis* Bursch, 1947.

Reference and locality ...		<i>G. mastelensis</i> Bursch 1947 Mollusk Id
Test		
Diameter (mm)		1–2 (2.2 max.)
Thickness (mm)		0.1–0.2 (0.3 max.)
Juvenile stages		
Proloculus	Diameter (μm)	—
Equatorial chambers	Width (μm)	—
	Height (μm)	40–70
Adult stage		
Lateral chambers	Width (μm)	90 max.
	Height (μm)	—
Tangential wall	Thickness (μm)	5–10
Lateral wall	Thickness (μm)	5–10
Pores	Diameter (μm)	5
Stolons	Diameter (μm)	10–15 (20 max.)

(Bursch 1947; Reiss and Hottinger 1984). Specimens from cored wells from Mururoa Atoll show similar chamber shapes as *Acervulina*. Chamber size is 60 μm . Reiss and Hottinger (1984) noted a more regular shape and arrangement of the chambers in *G. globulus* than in *Acervulina inhaerens*. *Sphaerogypsina* Galloway, 1933, was created for the species *Gypsina globulus* (Reuss, 1848).

Gypsina squamiformis (Text-fig. 4E; Table 7) is easily separated from the other *Gypsina* species since it is only formed by a single layer of arched chambers (Chapman 1900), which increase in size at the periphery of the encrusting test (Bursch 1947). Recent specimens described by Chapman (1900) from Funafuti have a test diameter of about 3–4 millimetres. The tangential walls of these chambers are perforated and large stolons allow communication between adjacent chambers (Bursch 1947). This species has been considered as a distinct genus, *Planogypsina* Bermudez, 1952.

TABLE 9. Size of main features of the test of *Gypsina saipanensis* Hanzawa, 1957.

Reference and locality ...		<i>G. saipanensis</i> Hanzawa 1957 Micronesia	
Test			
Diameter (mm)		1.7-2.6	
Thickness (mm)		0.25-0.60	
Juvenile stages			
Proloculus	Diameter (μm)	40	
Equatorial chambers	Width (μm)	—	
	Height (μm)	98-294	
Adult stage			
Lateral chambers	Width (μm)	50	
	Height (μm)	50	
Tangential wall	Thickness (μm)	—	
Lateral wall	Thickness (μm)	—	
Pores	Diameter (μm)	—	
Stolons	Diameter (μm)	—	

TABLE 10. Size of main features of the test of *Gypsina marianensis* Hanzawa, 1957.

Reference and locality ...		<i>G. marianensis</i> Hanzawa 1957 Micronesia	
Test			
Diameter (mm)		2.7	
Thickness (mm)		0.6	
Juvenile stages			
Proloculus	Diameter (μm)	120	
Equatorial chambers	Width (μm)	80-94	
	Height (μm)	120	
Adult stage			
Lateral chambers	Width (μm)	57	
	Height (μm)	57 (vent.) 10 (dors.)	
Tangential wall	Thickness (μm)	—	
Lateral wall	Thickness (μm)	—	
Pores	Diameter (μm)	10 (dors.)	
Stolons	Diameter (μm)	14 (vent.)	

G. mastelensis (Text-fig. 4F; Table 8), described by Bursch (1947), is composed of a basal layer of equatorial chambers, adherent to the substratum, and a dorsal arched zone. The juvenarium, situated at the centre of the equatorial layer, comprises three equatorial chambers. The next equatorial chambers are radially arranged around the embryonal chambers and their height generally increases towards the periphery of the test. There are also communications between the equatorial chambers through roof pores and stolons. The lateral chambers communicate with each other and with the equatorial chambers through stolons. Bermudez (1952) created the new genus *Hemigypsina* for this species.

The test of *G. saipanensis* (Text-fig. 4C; Table 9) may present a concavo-convex, or plano-concave, or discoidal shape, which gives it a uniform thickness or a thickened periphery. The test comprises an equatorial layer, two or three smaller chambers irregularly arranged on the ventral side, and a single layer of chambers

TABLE 11. Age, localities and systematic assignments of *Solenomeris* by previous authors.

Reference	Taxon	Age	Growth form	Locality	Systematic position
Trauth 1918	<i>P. planum</i>	Eoc.	Nodules	Austria	Acervulinidae
Douvillé 1924	<i>S. ogormani</i>	l. Eoc.	Nodules	S. France	Lithothamnidae
Douvillé and O'Gorman 1924	<i>S. ogormani</i>	l. Eoc.	Nodules	S. France	Calcareous algae
Pfender 1926	<i>S. douvillei</i>	l. Eoc.	Encrusting	N. Spain	Hydrozoan
	<i>S. sp.</i>	m. Eoc.		Italy	
Rao and Varma 1953	<i>S? douvillei</i>	l. Eoc.	Encrusting	Pakistan	Melobesiae
Maslov 1956	<i>S. afonensis</i>	Eoc.		Abkhazie	Similar to discocyclines and stromatopores
Elliott 1960	<i>S. douvillei</i>	Palaeoc.	?	Iraq	Solenoporaceae
	<i>S. ogormani</i>	l. Eoc.			
Johnson and Konishi 1960	<i>S. pakistense</i>	l. Eoc.		Pakistan	Solenoporaceae
Massieux 1961	<i>S. douvillei</i>	Eoc.	Reef	S. France	Incertae sedis algae
Schalekova 1963	<i>S. douvillei</i>	m. Eoc.	?	Slovakia	Calcareous algae
Elliott 1964	<i>S. ogormani</i>	Palaeoc. to	?	Iraq	Solenoporaceae
	<i>S. douvillei</i>	l. Eoc.			
De Zanche 1965	<i>Solenomeris</i>	Eoc.	Fragments	N. Italy	Melobesiae
Toumarkine 1966; 1967	<i>Solenomeris</i>	l. Eoc.	Reefs	S. France	
Hagn 1967	<i>Solenomeris</i>	l. Eoc.	?	Alps	Foraminifera
Hagn and Wellnhofer 1967	<i>Solenomeris</i>	u. Eoc.	Encrusting	Alps	Acervulinidae
Boulanger and Poignant 1969	<i>Solenomeris</i>	m. Eoc.	Encrusting	S. France	Algae
Terry and Williams 1969	—		?	Libya	Solenoporaceae
Poignant and Du Chaffaut 1970	<i>S. ogormani</i>	Palaeoc.	?	France	Incertae sedis algae
Hagn 1972	<i>G. ogormani</i>	Palaeoc.-Eoc.	Encrusting	Alps	<i>Gypsina</i>
Samuel <i>et al.</i> 1972	<i>S. sp.</i>	Maas.-Palaeoc.	?	Carpathians	Algae
Massieux 1973	<i>S. douvillei</i>	l. Eoc.	Reef and crusts	S. France	Incertae sedis algae
Poignant 1974	<i>Solenomeris</i>	u. Cret. l. Oligo.	?	?	Algae
Poignant and Blanc 1974	<i>S. ogormani</i>	u. Mio.		S. France	Solenoporaceae
Tambareau and Villatte 1974	<i>Solenomeris</i>	Eoc.	Encrusting	S. France	
Poignant 1976	<i>Solenomeris</i>	Eoc.	?	Spain	Red algae
Deloffre <i>et al.</i> 1977	<i>S. sp.</i>	Senonian	Fragments	Iran	Red algae
De Zanche <i>et al.</i> 1977	<i>Solenomeris</i>	Eoc.	Fragments	N. Italy	Solenoporaceae
Orszag <i>et al.</i> 1977	<i>S. douvillei</i>	Mio.	Encrusting	Turkey	
Poignant 1977	<i>S. sp.</i>	Palaeoc.	Fragments	Paris B.	Red algae
Wray 1977	<i>Solenomeris</i>	Palaeoc.	Encrusting	Libya	Solenoporaceae
Gaemers 1978	<i>Lithothamnium</i>	l. Eoc.	'ridges'	N. Spain	Melobesiae
Hagn 1978	<i>G. ogormani</i>	Palaeoc.-l. Eoc.	Encrusting	Alps	<i>Gypsina</i>

TABLE 11. (cont.)

Reference	Taxon	Age	Growth form	Locality	Systematic position
Dieni <i>et al.</i> 1979	<i>S. ogormani</i>	Palaeoc.-l. Eoc.	Fragments	Sardinia	Rhodophyceae
Hagn and Moussavian 1980	<i>G. ogormani</i>	Eoc.	Encrusting	Alps	<i>Gypsina</i>
Tappan 1980	<i>Solenomeris</i>	—	—	—	Solenoporaceae
Beckmann <i>et al.</i> 1982	<i>S. sp.</i>	Palaeoc.	Fragments	Italy	Solenoporaceae
Gravello and Ungaro 1982	<i>Solenomeris</i>	Eoc.	Fragments	Italy	Calcareous algae
Hagn 1983	<i>G. ogormani</i>	l. and m. Eoc.	Encrusting	Austria	<i>Gypsina</i>
Moussavian 1984	<i>G. ogormani</i>	u. Oligo.	—	Alps	<i>Gypsina</i>
Plaziat 1984	<i>S. douvillei</i>	l. Eoc.	Reef	S. France N. Spain	Probably encrusting Foraminifera
Perrin 1985	<i>Solenomeris</i>	l. Eoc.	Reef	S. France N. Spain	Acervulinidae
Betzler 1987	<i>Solenomeris</i>	l. Eoc.	?	N. Spain	Red algae
Brugnatti and Ungaro 1987	<i>Solenomeris</i>	Eoc.	Fragments	Italy	Calcareous algae
Eichenseer 1987	<i>Solenomeris</i>	l. Eoc.	'Ridges'	N. Spain	Red algae
Perrin 1987a, b, c	<i>Solenomeris</i>	l. Eoc.	Reef	S. France N. Spain	Acervulinidae
Perrin and Plaziat 1987					
Eichenseer 1988	<i>Solenomeris</i>	l. Eoc.	Crusts macroids 'ridges'	N. Spain	?
Betzler 1989	<i>Solenomeris</i>	l. and m. Eoc.	Encrusting	N. Spain	Red algae
Moussavian 1989	<i>Solenomeris</i>	Eoc.	—	Alps	<i>Acervulina ogormani</i>
Perrin 1992	<i>Solenomeris</i>	l. Eoc.	Crusts, macroids, and reefs	S. France N. Spain	Acervulinidae
Plaziat and Perrin 1992					

on the dorsal side. The equatorial layer includes a spherical proloculus surrounded by chambers with their diameter increasing towards the periphery (Hanzawa 1957).

Gypsina marianensis (Text-fig. 4D; Table 10), proposed by Hanzawa (1957), also has a plano-convex or concavo-convex shaped test which consists of three clearly distinct zones: median, dorsal and ventral. The median arched zone includes a spherical proloculus which is localized at the apex and a single layer of chambers with a spiral arrangement in the nepionic stage and an annular arrangement in the later neanic stage. Within this zone, each chamber shows two stolons at its opposite extremities. The dorsal zone is made of two or three layers of quadrangular depressed chambers (in axial section). The ventral zone is formed by several layers of chambers which tend to fill the hollow of the cone made by the median zone. The ventral chambers also show a depressed shape and generally a larger size than the median and dorsal chambers. The number of dorsal layers is always less than ventral layers (Hanzawa 1957).

Generic characteristics of *Gypsina*

This genus is represented by encrusting or free-living species. The proloculus has a spherical shape. The type species *Gypsina vesicularis* has a three-zoned test but in other species some zones may be absent. The dorsal zone, when present, does not show a well-developed unipolar growth but is represented by only a few layers of chambers. The chambers have walls a few microns in thickness and a perforated tangential wall. Species are discriminated according to the general shape of the test and the number and geometry of the different layers of chambers.

Growth pattern

Species of *Gypsina* may have free, attached or encrusting habits. *G. globulus* is a typical free-living species probably living on plants (Reiss and Hottinger 1984), while *G. squamiformis* develops thin crusts on hard substrates (Chapman 1900; Yabe and Hanzawa 1925; Bursch 1947; Reiss and Hottinger 1984). Several species show diversity in their growth habits. For example, *G. marianensis* shows a conical plano-convex or concavo-convex shaped test which is attached to the substratum but may sometimes extend across that surface and become encrusting (Hanzawa 1957). Bursch (1947) described specimens of *G. mastelensis*, a normally sessile and encrusting species, which adopts an irregular growth morphology when it becomes detached from its substratum during development.

Solenomeris

Identification of Solenomeris as a Foraminifera. *Solenomeris* has been referred to diverse groups of organisms, especially Rhodophyceae (Table 11). However, Trauth (1918) identified nodular forms of this organism from the Eocene of Austria (Province of Pongau) as the encrusting Foraminifera *Polytrema planum* (= *Acervulina inhaerens* var. *plana* according to Hanzawa 1957). Nevertheless, Trauth's publication was overlooked by subsequent authors until Hagn (1967). Thus, Douvillé (1924) created the genus *Solenomeris*, with the type species *Solenomeris O'gormanii* [sic] from the Early Eocene of the Béarn region (SW France). This author linked *S. ogormanii* to an isolated branch of Lithothamniae (Douvillé 1924, p. 170) while emphasizing the greater size of *Solenomeris* 'cells' compared with Lithothamniae. He did not assign the new genus to Solenoporaceae because of the difference in 'cell' shape in transverse section. In hand-specimens, these *Solenomeris* form 'small calcareous balls more or less mammilated with a smooth surface' (p. 169).

From the vicinity of Pau, Douvillé and O'Gorman (1924) described Eocene 'reefs' built up by *Solenomeris* associated with *Alveolina*, polystomelles and corals. However, these calcareous balls seem to be non-reefal material resedimented in deeper parts of the basin (Plaziat and Perrin 1992).

Pfender (1926) described another *Solenomeris*, *S. douvillei*, from the Early Eocene of the Spanish Pyrenees (Camarasa, Province of Lérida). According to Pfender, this species differs from the type species in its encrusting growth alternating with red algal crusts and never constitutes isolated calcareous nodules. Pfender (1926) recorded also *Solenomeris* sp. which forms 'globular masses' in the Middle Eocene of Vicentin (northern Italy). She compared *Solenomeris* with hydrozoans owing to the similar aspect of the 'tissue'.

Rao and Varma (1953) reported a new species, *S? douvillei* (non Pfender), from the Early Eocene of Pakistan. According to these authors, this species has an encrusting growth habit differing from *S. ogormanii* with smaller sized 'cells'. The place of *Solenomeris* among melobesians is paradoxically based on 'cell' sizes and on the more characteristic presence of conceptacles including reproductive cells (Rao and Varma 1953, p. 22); these structures correspond in fact to juvenile stages. The species of Rao and Varma (1953) was later named *Solenomeris pakistense* by Johnson and Konishi (1960).

Maslov (1956) described the new species *Solenomeris afonensis* (Early Eocene of Abkhazie) and noted the similarity of *Solenomeris* 'cells' with those of discocyclines and stromatopores.

The two species *Solenomeris ogormanii* and *S. douvillei* were recorded in the Paleocene and Early Eocene of Iraq by Elliott (1960) who placed them among Solenoporaceae. He argued that the algal nature of *Solenomeris* is supported by the existence of unipore conceptacles similar to those of Lithothamniae (Elliott 1964). However, Elliott (1964) underlined the rarity of reproductive organs and considered the conceptacles described by previous authors (Rao and Varma 1953; Maslov 1956) as Foraminifera belonging to the genus *Bullopore* subsequently encrusted by *Solenomeris*.

Most *Solenomeris* then have been misidentified as calcareous algae (Schalekova 1963; Boulanger and Poignant 1969; Poignant and Du Chaffaut 1970) and classified among Rhodophyceae (Samuel *et al.* 1972; Poignant 1975, 1977; Dieni *et al.* 1979; Deloffre *et al.* 1977; Garavello and Ungaro 1982) or more precisely among Solenoporaceae (De Zanche 1965; Terry and Williams 1969; Poignant and Blanc 1974; De Zanche *et al.* 1977; Wray 1977; Tappan 1980) or among Corallinaceae (Gaemers 1978).

Although some authors noted the resemblance of *Solenomeris* to discocyclines (Maslov 1956) or orbitoids (De Zanche 1965), Hagn (1967) was the first, after Trauth (1918), to refer *Solenomeris* from the Early Eocene ('Ilerdian') of the Bavarian Alps to the Foraminifera, comparing it with the acervulinid genera *Acervulina* and *Gypsina* (Hagn and Wellnhofer 1967). The genus *Solenomeris* was placed in the Family Acervulinidae and considered as a possible synonym of *Gypsina* (Hagn and Wellnhofer 1967).

Hagn subsequently used this new combination for Douvillé's species *Gypsina ogormani* (Hagn 1972, 1978, 1983; Hagn and Moussavian 1980; Moussavian 1984) because of the presence of a juvenarium similar to that of *Gypsina* (Hagn 1972, pp. 116–117), but without giving any illustration. Specimens from the Palaeocene and Eocene of the Bavarian and Austrian Alps show only encrusting growth forms, reworked in detrital facies (pebbles and blocks). Moussavian (1989) attributed *Solenomeris* to the genus *Acervulina* since he considered *Gypsina* to be a synonym of *Acervulina*. However, Brugnatti and Ungaro (1987) and Barbin *et al.* (1989) identified *Solenomeris* from the Middle Eocene of Northern Italy as *Gypsina*.

In spite of Hagn's publications, most other authors have not considered *Solenomeris* as a foraminifer and it is persistently placed among the red algae. So, in Tappan's synthesis of plant protists (1980), *Solenomeris* appears in the Family Solenoporaceae (p. 140).

Solenomeris douvillei from the Early Ypresian ('Ilerdian') of the Corbières (Southern France) forms reef-sized build-ups. It has been placed among *incertae sedis* algae by Massieux (1961, 1973), while the reefal *Solenomeris* from the Southern Pyrenees (Spain) were misidentified by Gaemers (1978) as *Lithothamnium* ridges. Beckmann *et al.* (1982) recorded *Solenomeris* from the Palaeocene of the Bergamo region (northern Italy) as Solenoporaceae but pointed out the problem of the algal nature of *Solenomeris* by referring to Hagn and Wellnhofer (1967).

The taxonomic problem of *Solenomeris* was pointed out by Plaziat (1984) without any conclusion in his palaeogeographical study of the Pyrenean region in which the different Eocene reefs of the Corbières and North-East Spain were described and interpreted for the first time from a palaeoecological perspective (Plaziat 1984).

Comparison of the structural features of the *Solenomeris* test with those of *Acervulina* from Pliocene-Quaternary reefs of Mururoa Atoll (French Polynesia) led to the conclusion that *Solenomeris* belonged to the Family Acervulinidae (Perrin 1985, 1987a). This was based on the identification of the juvenile stages with a geometry and arrangement of chambers which confirms assignation to the Family Acervulinidae (Perrin 1987a, 1987b; Perrin and Plaziat 1987). However, these juvenile stages were previously described and illustrated but misinterpreted as conceptacles (Rao and Varma 1953; Boulanger and Poignant 1969; Poignant and Du Chaffaut 1970; Poignant and Blanc 1974) or as the Foraminifera *Bullopore* sp. (Elliott 1964) or *incertae sedis* (Massieux 1973, pl. 26, fig. 5).

Stratigraphical range. *Solenomeris* is mainly reported from the Eocene, more rarely from the Palaeocene (Elliott 1960, 1964; Hagn 1972, 1978; Samuel *et al.* 1972; Beckmann *et al.* 1982). References to Late Cretaceous *Solenomeris* are rare. In the Senonian of Central Iran, Deloffre *et al.* (1977) reported fragments of *Solenomeris*, which however seem to be reworked. On the other hand, *S. ogormani* from the Upper Maastrichtian of Roquefort-Créon (Central Aquitaine) shows, according to Poignant and Blanc (1974), a significant build-up role. The *Solenomeris* sp. reported by Samuel *et al.* (1972) from the Maastrichtian and Montian-Thantetian of the Carpathians seem to grow in an encrusting habit. Poignant (1975) gave the stratigraphical range of *Solenomeris* as Upper Cretaceous to Upper Oligocene, with an acme during the Eocene. The youngest specimens of *Solenomeris* are from the Turkish Miocene (Poisson and Poignant 1975; Orszag-Sperber *et al.* 1977).

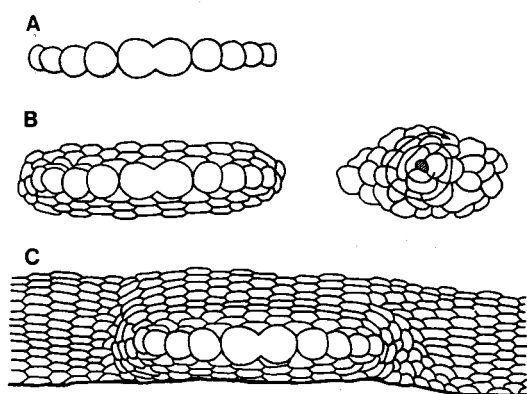
The development of *Solenomeris* reefs is so far known only from the Early Eocene (Lower Ypresian) of the Pyrenean region (Plaziat 1984; Plaziat and Perrin 1992).

Type species. The name of the type species *Solenomeris O'Gormani* described by Douvillé (1924) has been amended to *S. ogormani*. According to Douvillé (1924), *Solenomeris ogormani* is characterized by its growth as independent nodules and by a 'cell' ranging from 35 to 50 μm . The internal structure of the test consists of successive concentric layers of 'cells', some sections showing radial series of 'cells'. In transverse sections, these

have an irregularly hexagonal shape and thin walls, while in axial sections, they are arranged in vertical series, alternating from one series to the adjacent one, this resulting in hexagonal 'cells'. Some 'cells' are flattened (axial sections) and have been interpreted as resulting from slowed growth.

Solenomeris ogormani

The detailed reconstruction of *Solenomeris* development and its assignation to Foraminifera result from complementary observations using optical microscopy (thin and ultrathin sections) and scanning electron microscopy (fresh fractures or polished surfaces briefly etched with formic acid) of Ypresian specimens from the Pyrenees (*Solenomeris ogormani*) and from Plio-Quaternary reefs of the Mururoa atoll (*Acervulina inhaerens*, identification by M. Neumann in Répellin 1977; Perrin 1985, 1987a).



TEXT-FIG. 5. Juvenile stages of *Solenomeris* and beginning of encrusting adult stage (after Perrin 1987a). A, equatorial layer; B, ovoid stage in axial section (left) and in transverse section (right); C, test attached to a substratum and development of the crust; $\times 40$.

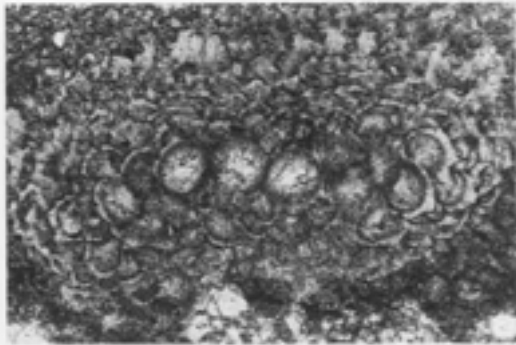
Juvenile stages. Juvenile stages of *Solenomeris* have often been observed in weakly developed incrustations, within the basal part of the crust. Only macrospheric forms (A), which are generally more frequent in all Foraminifera, have been observed (Text-fig. 5). They show the same characteristics and the same arrangement of chambers as the *Acervulina* from the Mururoa atoll (Pl. 2, figs 1–3; Perrin 1985, 1987a). In both cases, juvenile stages are localized close to the encrusted substratum and differ greatly from the adult stage in size, shape and arrangement of the chambers. The continuity in growth between juvenile and adult stages refutes the interpretation of a free living Foraminifera enclosed by acervulinids.

The equatorial layer (or equatorial disc) is formed by a planospiral arrangement of spherical or subspherical chambers of 65 to 70 μm diameter. In axial section, the equatorial disc is limited to seven to ten large rounded chambers whose diameter decreases towards the periphery (Pl. 2, figs

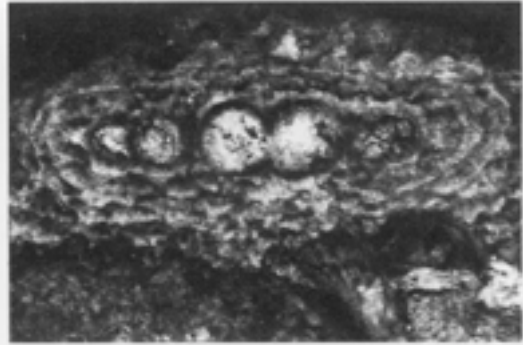
EXPLANATION OF PLATE 2

Figs 1–8. *Solenomeris*. Figs 1–3. Alaric Mountain, Aude, France, early Eocene. 1, juvenile stages in axial thin section; UPS Orsay Alaric 15,5; $\times 95$. 2, juvenile stages in axial thin section; UPS Orsay Alaric 13; $\times 170$. 3, juvenile stages in transverse thin section; UPS Orsay Villerouge; $\times 100$. Fig. 4. Isabena Valley, northern Spain, early Eocene; adult chambers in axial thin section; UPS Orsay Y1; $\times 95$. Fig. 5. Alaric Mountain, Aude, France, early Eocene; transverse thin section through the roofs and floors of adult chambers showing the pores and a sinuous chamber; UPS Orsay Alaric 15,3; $\times 195$. Fig. 6. Isabena Valley, northern Spain, early Eocene; axial thin section of adult chambers; mud infill aids the observation of roof pores in axial section; UPS Orsay Y1; $\times 115$. Figs 7–8. Albas, Aude, France, early Eocene. 7, SEM of subaxial section of adult chambers filled by a sparitic cement; UPS Orsay S2'; $\times 350$. 8, SEM of oblique section of adult chambers; UPS Orsay S3'; $\times 350$.

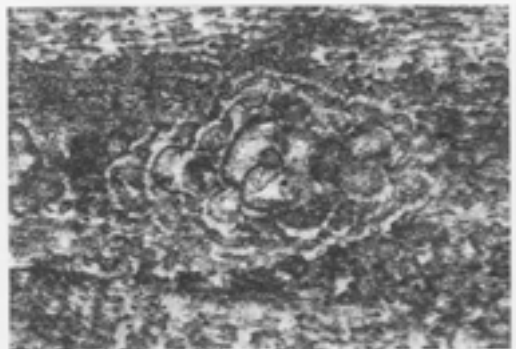
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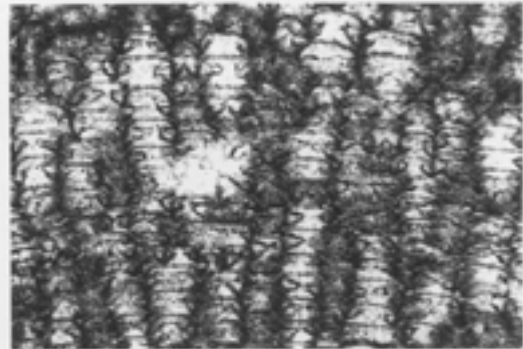
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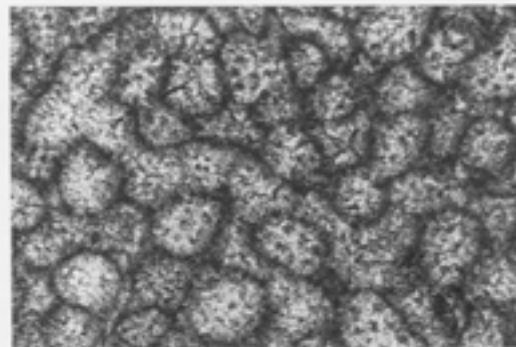
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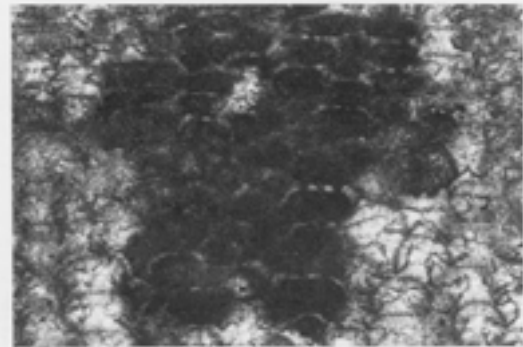
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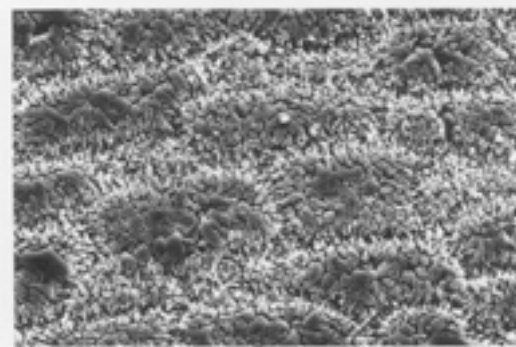
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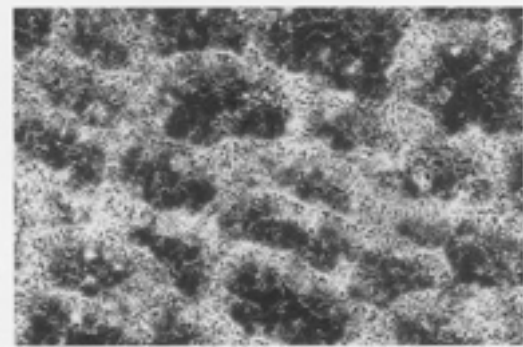
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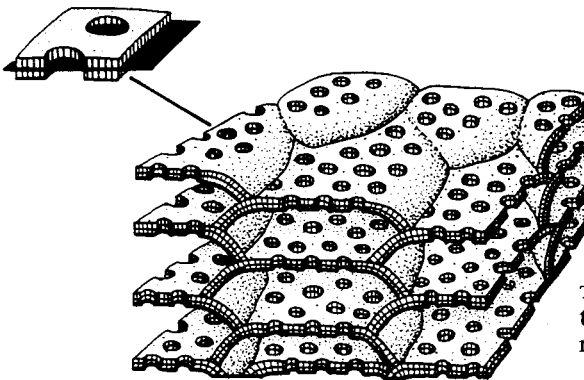


8

1–2). Transverse sections are very rare and show the spiral arrangement of the equatorial chambers (Pl. 2, fig. 3).

The lateral chambers have the same shape and size as the adult chambers and form in axial section a free bipolar growing ovoid as in *Acervulina inhaerens*.

Adult stage. The adult stage of *Solenomeris* is encrusting. The geometry and arrangement of adult chambers (Text-fig. 6) are similar to *Acervulina inhaerens*. In axial section, this kind of arrangement forms juxtaposed stacks of chambers, which are more or less perpendicular to the substratum and have been described by Douvillé as 'files of cells' (1924, pp. 169–170) (Pl. 2, figs 4, 7–8).



TEXT-FIG. 6. Adult stage of *Solenomeris* showing three-dimensional arrangement of chambers and microstructure of the tangential wall (after Perrin 1987a); $\times 400$.

In axial section, chamber height is *c.* 15–20 μm , while average width is 50–60 μm . Some isolated chambers are, however, larger but seem to be irregularly distributed.

In tangential section, the adult chambers have a rounded and irregular shape. Their average diameter is 60 μm (from 40 to 120 μm). Some chambers, having a much larger size, show very irregular, elongated sinuous shapes, their distribution being relatively random (Pl. 2, fig. 5).

Because encrustation is often more or less irregular, the growth direction of successive layers can change rapidly. This results in the gradual change from an axial to a tangential section through oblique sections which show more or less arched, typical chambers (Pl. 3, fig. 1). This vertical succession of differently oriented sections can often be observed in thin section and may give the illusion of a change in growth rate of the test. Thus, Moussavian (1989) described the axial and oblique sections as corresponding to two different kind of chambers which he misinterpreted, like Douvillé (1924), as the result of slow growth rate (= axial section) alternating with fast growth rate (= oblique section). This author also reported the presence of pillars in the external layers of the test, contributing to its strengthening. These pillars have never been observed in the tests of Pyrenean *Solenomeris*. On the other hand, calcitic cementation within the chambers is frequently observed both in *Solenomeris* and modern acervulinids and produces a thickening of the walls which, in axial sections, may be mistaken for the pillars described by Moussavian (1989).

The chamber walls, 5–7 μm thick, are characteristic of hyaline Foraminifera and are composed of two layers of fibrous hyaline calcite developed on both sides of a dark median layer.

The pores, 5–7 μm in diameter, are clearly visible in tangential sections through the roof of the chambers (Pl. 2, fig. 5) but hardly noticeable in axial section, except when chambers have been filled by carbonate mud (Pl. 2, fig. 6).

In ultrathin sections and in scanning electronic microscopy, the dark median layer of the tangential walls of Recent *Acervulina* appears to be continuous through the pores. In the Eocene *Solenomeris*, the dark layer is not preserved but its median location can be easily recognized and appears in scanning electron microscopy as a planar continuous void between the internal and external hyaline calcite layers.

The lateral walls are not perforated but the presence of stolons has been observed.

TABLE 12. Size of main features of the test of species of *Solenomeris*.

References and localities	Test		Juvenile stages					Adult stage	
	Ø (mm)	Thick-ness (mm)	Ovoid		Prolo-culus Ø (µm)	Equatorial chambers		Lateral chambers	
			Ø (µm)	Height (µm)		Width (µm)	Height (µm)	Width (µm)	Height (µm)
Trauth 1918									
<i>Polytrema planum</i>	1.6	0.36	—	—	—	—	—	60	—
Austria	4.7	1.76	—	—	—	—	—	80	—
Douvillé 1924									
<i>S. O'Gormani</i>	—	—	—	—	—	—	—	35	—
S. France	—	—	—	—	—	—	—	50	—
Pfender 1926									
<i>S. douvillei</i> N. Spain	—	—	—	—	—	—	—	30-45	20
<i>S. sp.</i> N. Italy	—	—	—	—	—	—	—	35-60	20-30
Maslov 1956									
<i>S. afonensis</i>	—	—	—	—	—	—	—	25-50	10-30
Abkhazie									
Rao and Varma 1953									
<i>S. douvillei</i> n. Pfender	—	0.03	280	72.8	—	31	31	—	13
Pakistan	—	1.7	412	115.5	—	78	78	—	—
Elliott 1964									
<i>S. ogormani</i>	—	—	—	—	—	—	—	40	26
Iraq	—	—	—	—	—	—	—	65	—
Boulanger and Poignant 1969									
<i>S. ogormani</i>	—	—	600	200	—	70	70	45	45
S. France	—	—	950	270	—	100	100	50	50
Poignant and Du Chaffaut 1970									
<i>S. ogormani</i>	—	—	420	180	—	40	40	80	35
Corsica France	—	—	—	—	—	—	—	100?	50
Poignant and Blanc 1974									
<i>S. ogormani</i>	—	—	600	200	—	70	70	40	—
S. France	—	—	950	270	—	100	100	50	—
Poisson and Poignant 1974									
<i>S. douvillei</i>	—	—	—	—	—	—	—	45	20
Turkey	—	—	—	—	—	—	—	50	25
Perrin 1987a									
<i>Solenomeris</i>	—	—	—	—	80	80	80	40	10
S. France N. Spain	—	—	—	—	—	—	—	100	20

Other species

Three other species of *Solenomeris* have been described (Table 12): *S. douvillei* Pfender, 1926; *S. (?) douvillei* Rao and Varma, 1953 (non Pfender) later called *S. pakistense* by Johnson and Konishi (1960), and *S. afonensis* Maslov, 1956.

Pfender (1926) separated her *Solenomeris douvillei* from *S. ogormani* by its encrusting habit, which never forms autonomous masses, and also reported a more zoned aspect of the test which corresponds in fact to a

succession of different sections (axial and oblique) and a development which seems a little bit different (Pfender 1926). The 'cell' size of *S. douvillei* is similar to that of *S. ogormani*: 30–45 μm in width and 20 μm in height.

Solenomeris piae, mentioned by some authors (Boulanger and Poignant 1969; Poignant and Blanc 1974), corresponds to a specimen from the Upper Cretaceous (?) of Cuba first described by Keijzer (1945) as *Solenopora piae*. In accordance with the photographs of Keijzer (1945), this organism appears to be a true solenoporacean alga and not a *Solenomeris*.

Rao and Varma (1953) described a new species from the Eocene of Pakistan which differs from *Solenomeris ogormani* by its encrusting habit and by a smaller size of its 'cells'. However, Rao and Varma (1953) compared the width of the 'cells' of *S. gormani* (i.e. 35–50 μm , according to Douville 1924) with the height of the 'cells' measured in their specimens (i.e. 13 μm and 18–40 μm). Moreover, these authors distinguished some larger 'cells' (18–40 μm high) in the internal zone of the 'thallus' and smaller 'cells' (13 μm high) in the external zone. Without doubt, both types of 'cells' correspond in fact to differently oriented chamber sections (oblique sections for larger 'cells' and axial sections for smaller 'cells'). Rao and Varma (1953) named this species *S. (?) douvillei*, a name preoccupied by *S. douvillei* Pfender, 1926 of which they seemed unaware. For this reason, Johnson and Konishi (1960) proposed the new name *Solenomeris pakistense*.

Lastly, the species *S. afonensis* was created by Maslov (1956) from Lower Eocene specimens of Novyj Afon in Abkhazie, but later Elliott (1964) and Poignant (Poisson and Poignant 1974) considered this species identical to *S. douvillei*. The width of the chambers ranges between 25 and 50 μm , while their height is between 10 and 30 μm . The thickness of the wall is c. 10 μm .

Generic characteristics of Solenomeris

The juvenile stages of *Solenomeris* show the development of a three-zoned free-living ovoid. During the earliest stages, the equatorial disc is characterized by the planospiral arrangement of subspherical equatorial chambers around the proloculus and the second perieubryonary chamber with an enlarged protochonical spiral (chambers decreasing in size). Afterwards, the ovoid is formed by addition of lateral chambers around this median equatorial disc.

The adult stage is encrusting and shows a unipolar growth on the dorsal side, characterized by the formation of successive layers of chambers alternating from one layer to the next one.

In axial section, adult chambers are subhexagonal, while in tangential section they have a rounded or more rarely sinuous elongated shape.

From the diagnosis given by different authors, the criteria of distinction at the specific level appear to be based first, on the encrusting or nodular habit and second, on the size of the chambers (so-called cells) (Tables 12–13).

Growth pattern

Encrustation. The attached stage of *Solenomeris*, as in other acervulinids, begins with close encrustation of a rigid substratum, developing with unidirectional formation of successive layers of chambers (Pl. 3, fig. 2). The thickness of such a crust varies from a few millimetres to several centimetres.

Development of branching form. In *Solenomeris*, contrary to other acervulinids, this encrusting growth may be followed by the development of branches, 1–2 centimetres in diameter. These

EXPLANATION OF PLATE 3

Figs 1–5. *Solenomeris*. Fig. 1. Isabena Valley, northern Spain, early Eocene; transition from tangential thin section (lower part of the photograph) to an axial section (top of the photograph); UPS Orsay Y1; $\times 35$.

Figs 2–3. Alaric Mountain, Aude, France, early Eocene. 2, early stage of an irregular crust; at the base of the crust, *Solenomeris* is interlayered with thin coralline crusts; UPS Orsay Sol. Alaric; $\times 5.5$. 3, thin section of a branch; UPS Orsay Sol. Alaric; $\times 6$. Figs 4–5. Corbières, Aude, France, early Eocene. 4, early stage of the branch development in thin section; the substratum consists of a coral fragment; UPS Orsay R15; $\times 6$.

5, early stage of the branch development in thin section, UPS Orsay R15; $\times 5.5$.

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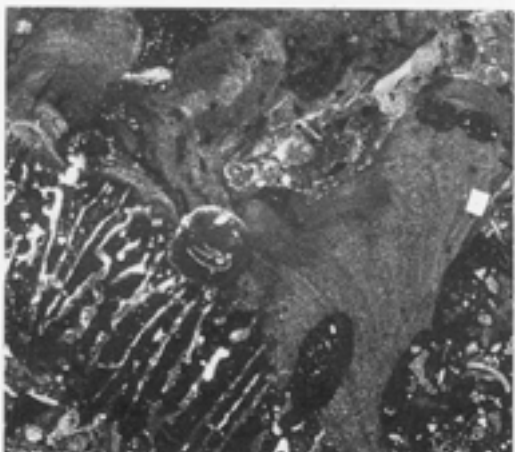
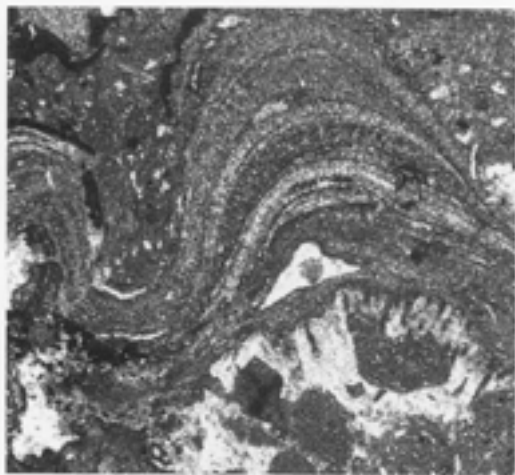
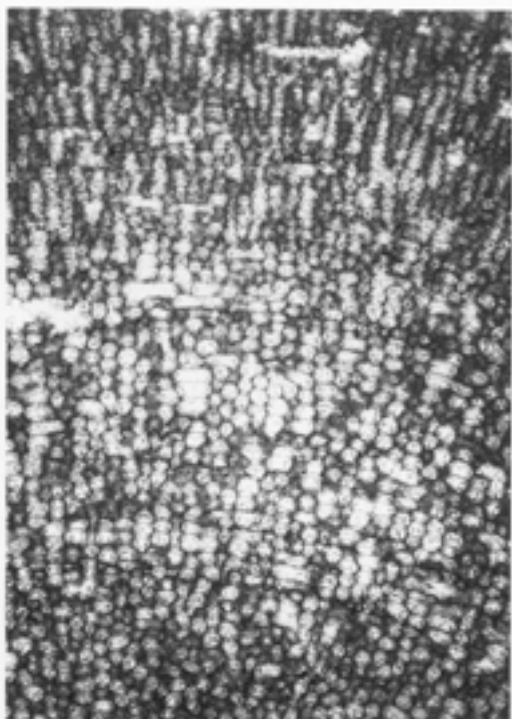
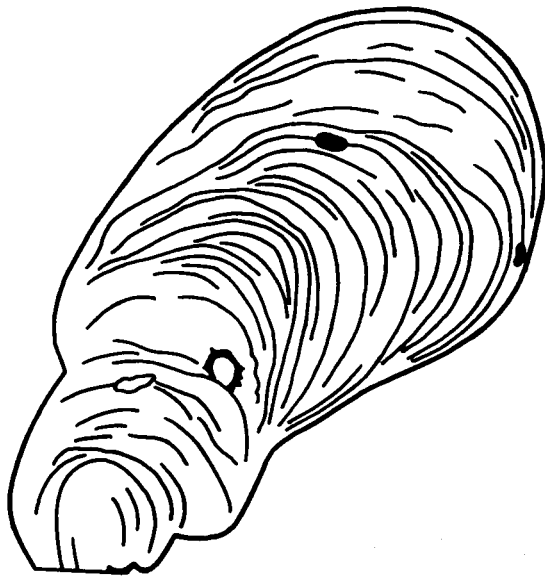


TABLE 13. Characteristics of species of *Solenomeris* described in the literature.

Species	Habit	Size of 'cells'	Comparisons
<i>S. O'Gormani</i> [sic] Douville 1924	Nodule	35–50 μm	Type species
<i>S. douvillei</i> Pfender 1926	Crust	30–45 μm width 20 μm height	More zoned than <i>S. O'Gormani</i> ; no individualized nodules; growth slightly different
<i>S. piae</i> Keijzer 1945	?	90–100 μm	'Cells' are twice as large as than in other species
<i>S?</i> <i>douvillei</i> non Pfender Rao & Varma 1953 = <i>S. pakistense</i> Johnson and Konishi 1960	Crust	External zone of the test: 13 μm height internal zone: 18–40 μm height	Differs from <i>S. ogormani</i> in the size of its 'cells' and in its encrusting habit
<i>S. afonensis</i> Maslov 1956	Crust	45–50 μm width 20–25 μm height	

TEXT-FIG. 7. Vertical section of a *Solenomeris* branch showing growth from highly convex-upwards cupolas at the top of the branch (traced from a microphotograph of thin section); *c.* $\times 3$.

closely-packed branches give buildups a massive aspect (Pl. 4, figs 1–3). In longitudinal thin sections, the banded structure made by the successive layers of chambers shows very convex domes covering the entire extremities of the branches and contributing at the same time to their thickening and their lengthening (Pl. 3, fig. 3; Text-fig. 7). Thus, the transverse sections of branches are characterized by tangential sections in their central part changing gradually towards the periphery to axial sections through intermediate oblique sections.

The development of branches is initially controlled by the morphology of the substratum, the convex irregularities of which influence the location of branch initiation (Pl. 3, figs 2, 4–5). On the other hand, the branches, which show a typical negative geotropism, can only develop if the substratum is stable, either as an originally stable substratum or a nucleus secondarily stabilized by

the weight of the thick *Solenomeris* crust. Thus, nodules (macroids sensu Hottinger 1983) resulting from the encrustation of a bioclast by *Solenomeris*, once stabilized, show a lower smooth surface, whereas the upper surface shows a progressive development of branches from initial swellings (Perrin 1992; Plaziat and Perrin 1992).

Bioherms. The buildups constructed by *Solenomeris* are massive domes with a metre-sized height and a more or less convex upward shape. These bioherms are made by the coalescent vertical branches of *Solenomeris*, with an oblique or fan-like growth at the edges of the buildups (Pl. 4, figs 3, 5) (Plaziat 1984).

Biostromes. A cluster of adjacent bioherms constitutes a reef, which is a typical biostrome. The spaces between the metric domal buildups is filled with a more or less sandy carbonate mud or with gravels consisting of broken branches of *Solenomeris* (Pl. 4, figs 4, 6). In the latter case, discrimination between the buildup and detrital parts is especially difficult in weathered outcrops. These biostromes can extend more than ten kilometres in length, with a thickness which can exceed ten metres (Plaziat 1984; Plaziat and Perrin 1992).

DISCUSSION

Identification of genera

The systematics of the Acervulinidae is relatively confused, especially at the generic level. Although Hanzawa (1931, 1947, 1957) and Bursch (1947) established precise specific criteria for the various species of *Acervulina* and *Gypsina*, discrimination between these genera does not seem to be really based on generic criteria. According to the definitions of Cushman (1950) and Loeblich and Tappan (1964), the diversity of size, shape and arrangement of the chambers would characterize the genus *Acervulina*; on the other hand, only *Gypsina* can include free-living spherical species. It seems difficult to base the distinction on the size of the lateral chambers and the irregularity of their arrangement. While the spherical shape of *Gypsina globulus* may be a specific characteristic, the shape of the test in the other acervulinids is too variable, especially in encrusting forms, to be used for the identification of the different genera. However, *Gypsina* appears to be represented by species of smaller size made of a limited number of layers of chambers.

According to Hanzawa (1931, 1940, 1947, 1957) and Bursch (1947), the test of acervulinids appears to consist of three clearly different zones which can be recognized in axial sections: a median layer or equatorial zone, formed by the equatorial disk during the juvenile stages, which is enclosed between a dorsal zone and a ventral zone. Some of these three zones may be absent in some species of *Gypsina*. On the other hand, all three are always present in *Borodinia* and *Acervulina*. The number of layers of chambers within the ventral and dorsal zones changes in accordance with the different forms of acervulinids. Only the equatorial zone, when it exists, is constantly represented by a single layer of chambers. The number of distinct zones constituting the test, and the number of layers within the ventral and dorsal zones, appear to be the diagnostic criteria distinguishing *Gypsina* from *Acervulina* and *Borodinia*.

A third criterion seems especially reliable for generic discrimination. This concerns the thickness of the tangential walls (roofs and floors of the chambers) which is relatively constant within a genus. Thus, *Acervulina* and *Gypsina* are both characterized by thin tangential walls, whose thickness varies between a few microns and 25 μm . On the other hand, the thickness of the roofs in *Borodinia* is more than 100 μm (140 μm in the species described by Hanzawa 1957).

A combination of these three criteria provides a relatively easy and reliable method for separating the genera in the Acervulinidae (Table 14). *Acervulina* is only represented by encrusting forms with a three-zoned test. The dorsal zone always comprises several layers of chambers, whose number is much higher than that of the ventral zone. The tangential walls are thin (5–25 μm). *Borodinia* possesses three distinct zones, the dorsal one always including several layers of chambers. The tangential walls are thicker than 100 μm . *Gypsina* includes both free and encrusting forms with a

test consisting of one, two or three distinct zones. The dorsal zone, when it exists, is formed by one single, or a few layers of chambers, the number of dorsal layers always remaining lower or equivalent to that of the ventral zone. The tangential wall of chambers is thin (5–25 μm).

The use of these criteria requires observation of the test in axial sections passing through the ovoid of juvenile stages in order to distinguish the different zones. It is not necessary to have a section of the proloculus for the identification of acervulinids at the generic level. However, a precise measurement of the tangential walls must be taken in axial section and not in oblique sections. This can be made difficult by diagenesis, especially when the chambers have been cemented by fibrous calcite which it is critical to distinguish from the fibrous walls of the chambers. Nevertheless, the difference in thickness between the thin tangential walls (5–25 μm) of *Gypsina* and *Acervulina*, and the thick walls of *Borodinia* (more than 100 μm) is important enough to constitute an especially reliable and easy to use criterion of identification at generic level.

Identification of species

Species of *Gypsina* may be easily distinguished according to the number of zones (ventral, median or equatorial, and dorsal), and the number of layers of chambers within each of these zones.

Borodinia is only represented by a single species: *Borodinia septentrionalis* described by Hanzawa (1940, 1957). The presence of the three zones constituting the test and the larger thickness of the walls are criteria characterizing the genus. The species is distinguished by spatuliform chambers in tangential sections (Hanzawa 1957).

In *Acervulina*, the criteria which may be used for species identification are the morphology of the roof of the chambers in axial section and the shape of some chambers in tangential section. *A. linearis* is characterized by roofs of the lateral chambers of the same layer forming a continuous straight line in axial section. However, in the other species, the adult chambers have roofs which are separate from each other. In tangential section the lateral chambers of *A. linearis* have angular shapes while those of *A. inhaerens* are rounded. *Acervulina (Ladoronia) vermicularis* shows large sinuous chambers in tangential sections.

Validity of species of Solenomeris

The distinction between different species of *Solenomeris* is based on two criteria: growth habit and size of the adult chambers ('cells') (Table 13). The growth forms, as in many sessile organisms, depend directly on environmental factors: morphology of the substratum, hydrodynamics and competition with other organisms. Their morphology also changes during the development of an individual. Branching *Solenomeris* necessarily begins after an encrusting stage. In the same way, macroids from the Corbières show a primary concentric encrustation stage and, after the stabilization of the nodule by its own weight, begin to develop branches on the upper side (Perrin 1992; Plaziat and Perrin 1992). Therefore, the growth habit of the organism does not appear to be a reliable criterion for the identification of species.

EXPLANATION OF PLATE 4

Figs 1–6. *Solenomeris*. Figs 1–3. Alaric Mountain, Aude, France, early Eocene. 1, outcrop view showing the closely packed branches of *Solenomeris* on a weathered surface. 2, branches in growth position; note the presence of scarce muddy sediment between branches (photograph width is c. 30 cm). 3, detail of a *Solenomeris* bioherm showing bivalve borings filled with muddy sediment, (photograph width is c. 35 cm). Fig. 4. Albas reef, Aude, France, early Eocene; fragments of branches in a muddy sediment. Figs 5–6. Alaric Mountain, Aude, France, early Eocene. 5, detail of a *Solenomeris* bioherm showing the vertical or oblique growth of branches. 6, part of a *Solenomeris* reef showing the cluster of adjacent bioherms and locally the muddy infill between the bioherms (photograph width is c. 4 m).

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The dimensions of the chambers, diagnostic data for palaeontologists treating *Solenomeris* as an alga, are difficult to compare when axial and transverse sections have not been distinguished. On the other hand, authors considering *Solenomeris* as a foraminifer do not specify the size of the chambers (Hagn 1967; Hagn and Wellnhofer 1967; Moussavian 1989). Thus, the heights of the chambers in different *Solenomeris* descriptions are especially difficult to interpret since measurements may have been taken in oblique sections and are therefore overestimated. This is certainly the case for the sizes reported by Rao and Varma (1953) who distinguished between smaller sized 'cells', located in the external part of the test, and larger 'cells' situated in the internal zone (Table 13). These correspond respectively to axial sections and oblique sections of the same type of chambers. Without taking into account the measurements of the larger chambers reported by Rao and Varma (1953), the height of chambers appears to vary between 13 μm in *S. pakistense* (Rao and Varma 1953) and 30 μm in *Solenomeris* from the Middle Eocene of northern Italy (Pfender 1926). In the studied samples from the Early Ypresian of the Corbières and northern Spain, average height varies from 15 to 20 μm and ranges between 10 and 35 μm . However, even if previous authors gave overestimated dimensions, the variability in height of chambers in all the so-called species of *Solenomeris* shows the same range of size as the variability which exists at the specific level in *Acervulina* and *Gypsina*. For example, the height of chambers can vary from 5 to 25 μm in *G. vesicularis* (Bursch 1947; Hanzawa 1957), from 5 to 47 μm in *A. inhaerens* (Hanzawa 1931, 1957), and from 11 to 50 μm in *A. linearis* (Hanzawa 1947, 1957) (Tables 1–2, 5).

On the other hand, the width of the chambers seems to be quite similar in the four species *Solenomeris ogormani*, *S. douvillei*, *S. pakistense* and *S. afonensis* and varies from 25 to 50 μm . *Solenomeris* from southern France and northern Spain have lateral chambers whose size varies from 40 to 100 μm , with an average of 60 μm . Moreover, some tangential sections show the presence of sinuous larger chambers whose length can reach 250–300 μm . However, these large-sized chambers are relatively rare and are seldom reported in previous descriptions of *Solenomeris* (Perrin 1985, 1987a). In *Acervulina* and *Gypsina*, the variability of chamber width within the same species is important, especially in *G. globulus* (60–180 μm) and in *A. inhaerens* (50–230 μm).

Therefore the size of the adult lateral chambers does not seem to be a reliable criterion for distinguishing different species of *Solenomeris* because of the large intraspecific variability of this feature in the acervulinids. Some authors have synonymized the different species of *Solenomeris* but without any discussion (Elliott 1964; Boulanger and Poignant 1969; Poignant and Blanc 1974; Moussavian 1989).

Comparison between Solenomeris and other Acervulinidae

The test of *Solenomeris* is typically composed of three distinct zones: a ventral zone formed by the lateral chambers of the ovoid, juvenile stages; a median or equatorial zone comprising a single layer of chambers which constitutes the equatorial disc including the proloculus; and a dorsal zone made of numerous layers consisting of lateral chambers of the juvenile stages and chambers of the adult stage which constitute the bulk of the construction.

The tangential walls of *Solenomeris* are thin (5–10 μm). These characteristics of *Solenomeris* appear closer to the genus *Acervulina* than to any other member of the Acervulinidae.

In axial section, the roofs of the lateral chambers in *Solenomeris* never form a continuous line like *A. linearis*, but appear clearly individualized (when skeletal preservation is good enough). Tangential sections mainly show rounded chambers but with scarce larger and sinuous chambers similar to those of *A. vermicularis*. Thus, *Solenomeris ogormani* differs both from *Acervulina inhaerens* and *A. (Ladoronia) vermicularis* since its test comprises, in tangential section, not only rounded lateral chambers but also large sinuous chambers (Table 14).

Moussavian (1989) united the different species of *Solenomeris* as *Acervulina ogormani* instead of *Gypsina ogormani* (Moussavian 1984) because he believed that the genera *Acervulina* Schultze, 1854 and *Gypsina* Carter, 1877 were synonymous, *Gypsina* being the junior synonym. Nevertheless, Moussavian suggested that an extensive revision of this family was necessary. The synonymy of *Acervulina* and *Gypsina* is also based on the long-recognized synonymy of the species *A. inhaerens*

TABLE 14. Key to main genera and species of Acervulinidae.

A	Test free or encrusting, consisting of one, two or three distinct zones; dorsal zone, when present, comprising one or a few layers of chambers; thin tangential walls (5–25 μm)	<i>Gypsina</i>
A1	One single zone	
	● Equatorial zone: one single layer	<i>G. squamiformis</i>
	● Equatorial zone absent	<i>G. globulus</i>
A2	Two zones	
	● Equatorial zone: one single layer of chambers and dorsal zone	<i>G. mastelensis</i>
A3	Three zones	
	● Equatorial zone: one single layer of chambers Ventral and dorsal zones: equal number of layers	<i>G. vesicularis</i>
	● Equatorial zone: one single layer of chambers Ventral zone: a few chambers Dorsal zone: one single layer	<i>G. saipanensis</i>
	● Equatorial zone: one single layer of chambers Ventral zone: several layers of chambers Dorsal zone: two or three layers	<i>G. marianensis</i>
B	Test encrusting, consisting of three distinct zones: a ventral zone, an equatorial zone and a dorsal zone; dorsal zone comprising several layers of chambers	
B1	Thick tangential walls (> 100 μm)	<i>Borodinia</i>
	● Some chambers showing a spatuliform shape in tangential section	<i>Borodinia septentrionalis</i>
B2	Thin tangential walls (5–25 μm); juvenile stages with equatorial chambers increasing in size towards the periphery of the equatorial disc	<i>Acervulina</i>
	● Roofs of chambers of the same layer forming a continuous straight line in axial section; chambers more or less angular in tangential section	<i>Acervulina linearis</i>
	● Roofs of chambers of the same layer do not form a continuous straight line in axial section; tangential section showing only rounded-shaped chambers	<i>A. inhaerens</i>
	● Roofs of chambers of the same layer do not form a continuous straight line in axial section; tangential section showing sinuous large chambers	<i>A. (Ladoronia) vermicularis</i>
B3	Thin tangential walls (5–25 μm); juvenile stages with equatorial chambers decreasing in size towards the periphery of the equatorial disc	<i>Solenomeris</i>
	● Roofs of chambers of the same layer do not form a continuous straight line in axial section; most of the chambers of tangential section show a rounded shape but scarce sinuous large chambers are also present	<i>Solenomeris ogormani</i>

and *G. plana*. Hanzawa (1957) considered *G. plana* as a variety of *A. inhaerens*: *Acervulina inhaerens* var. *plana*. However, the type species of *Gypsina* is not *Polytrema planum* = *Gypsina plana* Carter, 1877, as indicated by Loeblich and Tappan (1964), but *Gypsina vesicularis* Parker and Jones, 1860. Moreover, from the above review of the geometrical characteristics of the test, both *Acervulina* and *Gypsina* appear clearly different and can be easily distinguished by the number of zones constituting

the test and by the number of layers of chambers within the dorsal and ventral zones. It is therefore difficult to place the different species of *Solenomeris* within any particular genus without first carefully studying the geometrical features of their internal structure.

CONCLUSIONS

The foregoing critical review of growth organization and chamber morphologies in *Acervulina*, *Borodinia*, *Gypsina* and *Solenomeris* suggests reliable and easily identifiable criteria for the discrimination of different genera and species (Table 14). The genus *Solenomeris*, recently included in the Acervulinidae (Hagn 1967; Perrin 1985, 1987a), is certainly closely related to the genus *Acervulina*. However, the morphology of the roof of the chambers in axial section, the occurrence of numerous rounded lateral chambers and also of large sinuous chambers distinguish clearly *Solenomeris* from species of *Acervulina*. Thus also taking into account the form of the juvenile with its enlarged protoconchal spiral, it would seem appropriate to regard *Solenomeris* as a separate genus within the Acervulinidae.

Previously described species of *Solenomeris* seem to be identical because their discrimination is based on unreliable criteria; their geometry and the internal structure of the test having been misinterpreted as those of a red alga.

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