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An example of auto-mobility and host substrate relationship in *«Cycloseris» escosurae* Mallada, 1887, scleractinian coral from Lower Aptian of Spain

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ABSTRACT – «Cycloseris» escosurae *is an Early Aptian solitary coral from Spain created by Mallada (1887). The taxonomic revision indicates that the species of Mallada shows intermediate characters between the genus* Cycloseris *Lamarck and* Cyclophyllopsis *Alloiteau, 1959, and, may be, it is pertaining to a new genus. This small, discoidal coral is commonly settled on* Palorbitolina *tests and, occasionally, on bivalve fragments, Conchostracan shells, and others. Few specimens do not display apparent attachment. The hypothesis of Alloiteau (1952) concerning an association of Eocene solitary corals to macroforaminifera as a case of commensal relationship is here discussed. Architectural criteria for self induced mobility, such as trabeculae directed also basally and the lack of epitheca, as demonstrated within Recent* Cycloseris cyclolites *(Lamarck) suggest that the species from Spain had been auto-mobile (Gill & Coates, 1977). The relationship between the coral and its host substrate is analyzed.*

RIASSUNTO – [Un esempio di auto-mobilità e rapporti di relazione con il substrato ospite in *«Cycloseris» escosurae* Mallada 1887, esacorallo dell'Aptiano inferiore della Spagna] – «Cycloseris» escosurae *è un corallo solitario istituito da Mallada (1887) nell'Aptiano inferiore della Spagna. La revisione tassonomica indica che la specie di Mallada mostra caratteri intermedi tra il gen.* Cycloseris *Lamarck e* Cyclophyllopsis *Alloiteau, 1959, e forse è attribuibile ad un nuovo genere.*

Questo piccolo corallo discoidale si rinviene generalmente attaccato su gusci di Palorbitolina *e, più raramente, su frammenti di bivalvi, conchiglie di Concostraci e altro. Pochi esemplari non mostrano evidenze di attaccamento. Viene discussa l'ipotesi di Alloiteau (1952), relativa ad un'associazione di coralli solitari e macroforaminiferi dell'Eocene, interpretata come un caso di commensalismo. Criteri architettonici indicanti capacità di mobilità effettuata dallo stesso, come trabeculae dirette anche verso la base e l'assenza di epiteca, come è dimostrato nella forma recente* Cycloseris cyclolites *(Lamarck), suggeriscono che la specie proveniente dalla Spagna era auto-mobile. Viene infine analizzata la relazione esistente tra il corallo ed il suo substrato.*

INTRODUCTION

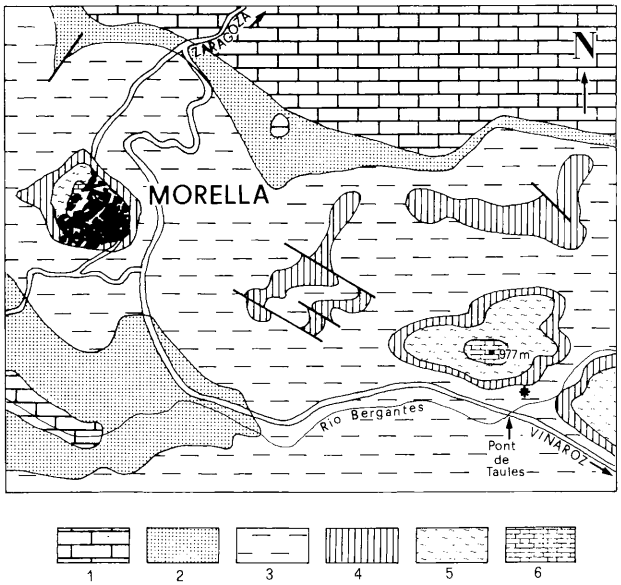
The paper describes a particular association between a small, discoidal, free solitary scleractinian coral, *«Cycloseris» escosurae* Mallada, 1887, from the Early Aptian of Spain, and its larval settling base constituted mainly by Palorbitolinas. The distinctive morphology of this coral suggests a mobile, free-living habit upon particular substrates, and calls for a new taxonomic position.

In literature there are several examples concerning living and fossil corals which settle upon particular substrate hard particles, including skeletons of other organisms (Knight-Jones, 1951; Crisp & Meadows, 1967; Scheltema, 1974; Gray, 1974; and others). Some authors demonstrate substrate specificity among living and fossil corals, inferring to the existence of a commensal or symbiotic relationship (Clarke, 1908; Alloiteau, 1952; Brett & Eckert, 1982; Meyer & Ausich, 1983; Darrell & Taylor, 1993; and others). Gill & Coates (1977) described in detail the relationship between skeleton morphology and the type of mobility. The fossil species *«Cycloseris» escosurae* will be compared with *Cycloseris cyclolites*, a Recent and certainly mobile species.

PROVENANCE AND STRATIGRAPHIC POSITION OF THE STUDIED MATERIAL

Cycloseris escosurae was described by Mallada (1887) from the «Urgo-aptense» of Morella (Prov. Castellon, eastern Spain). No exact locality and stratigraphic position were given by that author. The material of *«Cycloseris» escosurae* studied in this paper comes from the Pont de Taules, a bridge along the Morella - Vinaroz road, crossing the Bergantes river approx. 3 kms southeast of Morella (Text-fig. 1). Isolated specimens were collected on the southeastern slope of the 977 m hill in soft, grey marls containing abundant *Palorbitolina lenticularis* (Blumenbach), which are exposed north of this bridge along the path running parallel to the Bergantes river. Also a pebble of a packstone with silty matrix, found in the river-bed near the bridge yielded numerous specimens of *«C.» escosurae*, as well as gastropods, bryozoans, echinoid spines, bivalve fragments, and abundant, obviously reworked shells of fresh or brackish water Conchostraca.

The stratigraphic sequence exposed on the southern slope of 977 m hill was firstly described in detail by Marie (1964):



Text-fig. 1 - Geological sketch of the Morella area (after Marie, 1964; lithological nomenclature after Salas, 1987) showing the locality (asterisk) of *«Cycloseris» escosurae* Mallada. Scale 1:25.000.
1) Artoles Formation (limestones and marls; Barremian). 2) Morella Formation (shales and sandstones; lowermost Aptian). 3-5) Forcall Formation (marls and marly limestones; Lower Aptian) (3: Cap de Vinyet Member; 4: Barra de Morella Member; 5: Morella la Vella Member). 6) Villarroya Formation (massive limestone; Upper Aptian).

6. Massive, white Urgonian limestone forming the top of the hill.

5. Grey, clayey marls, very fossiliferous, containing *Plicatula placunea* Lam., *Ostrea aquila* d'Orb., abundant *Burrirhynchia miliani* (Bat.), and ammonites (40 m.).

4. Massive, fossiliferous limestone with *Palorbitolina lenticularis* (Blum.), abundant terebratulids (*T. sella* Sow., *T. daphne* Coq., *T. lentoidea* Leym.) and rhynchonellids [*Burrirhynchia miliani* (Bat.)], echinoderms (*Heteraster couloni* d'Orb., *Salenia mamillata* Cott., and ammonites (*Deshayesites* sp., Aconeceratidae) (2 m.).

3. Nodular, marly limestone with *Palorbitolina lenticularis* (Blum.) (15 m).

2. Massive limestone with large *Palorbitolina lenticularis* (Blum.), which has yielded at its top a specimen of *Deshayesites* aff. *consobrinus* d'Orb. (40 m.).

1. Nodular marls with abundant *Palorbitolina lenticularis* (Blum.), gastropods, lamellibranchs, and *«Cycloseris» escosurae* Mallada (40 m.).

This unit yielded the specimens studied in the present paper. A comparison between this section and the actual lithostratigraphic subdivision of the Aptian in the Morella region (Canérot *et al.*, 1982; Salas, 1987) reveals that units 1 to 5 belong to the Forcall Formation, which is composed of three members (from bottom to top): Cap de Vinyet Member (corresponding to unit 1), Barra de Morella Member (= unit 2), and Morella la Vella Member (= units 3 to 5). The Urgonian limestone at the top of 977 m hill (= unit 6) corresponds to the Villarroya Formation. Abundant *«Cycloseris» escosurae* occur also in soft grey marls with *Palorbitolina lenticularis* (Blum.), which are exposed approx. 2 kms northwest of Morella at Cap de Vinyet, the type-locality of the member of the same name.

Numerous authors (Marie, 1964; Canérot *et al.*, 1982; Martinez *et al.*, 1994) have pointed out that the Forcall Formation as a whole can be dated by means of ammonites as Lower Aptian. Marin & Sornay (1971) published a list of ammonites from the «Marnes à Plicatules» (corresponding at least partially to unit 5 of the section of 977 m hill) in the Morella and Forcall region; this association indicates the middle part of the Lower Aptian («Bédoulien moyen»; *deshayesi*-Zone). The underlying beds containing *«Cycloseris» escosurae* can be therefore assigned to the lower part of the Lower Aptian.

SPECIFIC SUBSTRATE CHOICE

Among corals, some living scleractinians (*Heteropsammia, Heterocyathus* and *Psammoseris*) are known to encrust dead gastropod shells, which is, in turn, become occupied by a sipunculid worm, *Aspidosiphon*, establishing a symbiotic relationship (references *in* Gill & Coates, 1977; Darrell & Taylor, 1992). *Caryophyllia smithi*, another Recent solitary coral, prefers to encrust *Ditrupa*, but also shells of *Aporrhais* and *Dentalium*; it is mentioned as an example of intergrowth symbiosis (Wilson, 1976; Darrell & Taylor, 1993).

Silurian, Devonian and Carboniferous corals (*Heliolites, Favosites, Antholites, Emmonsia, Cladochonus*, etc.) occasionally encrusted almost exclusively stems of certain large crinoids (Hudson *et al.*, 1966; Kase, 1986; McIntosh, 1980; Darrell & Taylor, 1993), while others (*Heliolites, Favosites, Michelinia, Pleurodictyum, Hyostragulum*, etc.) may settle upon gastropods, nautiloids, hyolitids, boring bivalves and pebbles (Nicholson & Etheridge, 1880; Clarke, 1908; Barthel & Barth, 1972; Marek & Galle, 1976; Brett & Cottrel, 1981; Kase, 1986; Baird *et al.*, 1989; Darrell & Taylor, 1993).

Gill & Coates (1977) summarize the highly specialized and distinctive mode of life, by sipunculid «towing», of *Heteropsammia* and *Heterocyathus*

and other corals which live in a similar way upon soft muddy sand to sand substrates.

For associations of some solitary, discoidal scleractinian corals with macroforaminifers, Michelin (1840-47) seems to have been the first to illustrate *Cyclolites borsensis* and *Cyclolites semiglobosa*, from the Eocene of Palarea, France, attached to macroforaminifers. Since Michelin, several other authors have described associations of *Funginellastraea, Cyclolitopsis* (referred to as *Cyclolites* or *Cycloseris*) and other discoidal corals with macroforaminifera belonging to discocyclinid or nummulitid groups from the Eocene of Spain, France, Northern Italy, India, Borneo, Indonesia, etc. (Table 1).

Alloiteau (1952) and Barta Calmus (1973) inferred to a commensal relationship to explain this specific basal attachment, while Ruiz de Gaona (1944) concluded that the corals were «guests» of the macroforaminifers. Busquets & Vilaplana (1986), on

Species	Substrate	Age	Authors
Chomatoseris	Any hard particle	Middle Jurassic	Gill, 1970; Gill & Coates, 1977
Genabacia	Any hard particle	Middle Jurassic	Gill, 1972
Cycloseris blanckenhorni	Undetermined	Cenomanian, Lebanon	Felix, 1913
Cycloseris provincialis	Undetermined	Turon. - Santon., Le Beausset (France)	de Fromentel, 1870
Cyclolites borsensis	Macroforam.	Eocene, La Palarea (France)	Michelin, 1840-47
Cyclolites semiglobosa	Macroforam.	Eocene, La Palarea (France)	Michelin, 1840-47
Cyclolites andianensis	Macroforam.	Eocene, Biarritz (France)	d'Archiac, 1847
Cyclolites lenticularis	Macroforam.	Eocene, Biarritz (France)	d'Archiac, 1847
Cycloseris perezi ?	*Nummulites*	Eocene, Borneo	Fritsch, 1878
Funginellastraea heberti	*Operculina, Discocyclina sella, D. pratti, D. olianae*	Eocene; Cuebris and Allons (France); Buda (Hungary); Castelloli (Spagna); S. Giovanni Ilarione, Grancona, Possagno (Italy)	d'Achiardi, 1867; Reuss, 1874; Solé Sabaris, 1942; Almela *et al.*, 1943; Ruiz de Gaona, 1944; Tournouer, 1872; Oppenheim, 1900; Barta Calmus, 1973; Russo, 1979, 1980
Funginellastraea barcelonensis	*Discocyclina, Asterodiscus stellaris*	Eocene, Castelloli (Spagna)	Oppenheim, 1911; Busquets and Vilaplana, 1986; Alvarez Peres, 1993
Cyclolitopsis patera	*Discocyclina applanata, Aktinocyclina radians, Assilina*	Middle-Upper Eocene; S. Giovanni Ilarione, Brazzano, Possagno (Italy); Allons, Entrevaux, Collengues (France); Gabardiella (Spagna)	Dainelli, 1915; d'Achiardi, 1867; Tournouer, 1872; Ruiz de Gaona, 1944; Oppenheim, 1900; Barta Calmus, 1973; Russo, 1979, 1980
Protocycloseris vinassai	*Nummulites, Operculina ammonea*	Eocene; Possagno (Italy)	Oppenheim, 1900; Russo, 1979
«Petalopsammia gurreai» (?Cyclolitopsis patera)	*Nummulites*	Eocene; Puebla de Fontova (Spagna)	Reig Oriol, 1988
Bathyactis eocenica	*Discocyclina dispansa*	Lower Eocene; Nanggoelan, Giava (Indonesia)	Gerth, 1933
Trochocyathus nummuliticus	*Nummulites*	Lower Eocene; Ranikot Series of Sind	Duncan, 1880
Leptocyathus epithecata	*Nummulites*	Lower Eocene; Ranikot Series of Sind	Duncan, 1880
Trochocyathus burnesi	*Nummulites*	Upper Eocene-Oligocene; Nari Series of Sind	Duncan, 1880
Blanfordia nummiformis	*Nummulites*	Upper Eocene-Oligocene; Nari Series of Sind	Duncan, 1880
Cyclolites rhomboidus	*Nummulites*	Eocene, Dubrowitza near Scandona (Dalmazia)	Oppenheim, 1901
Cycloseris brazzanensis	*Nummulites*	Eocene, Brazzano near Cormons (Friuli)	Oppenheim, 1901
Cycloseris minima	*Nummulites*	Eisenrichterstein near Hallthurm (Nördliche Kalkalpen)	Darga, 1992

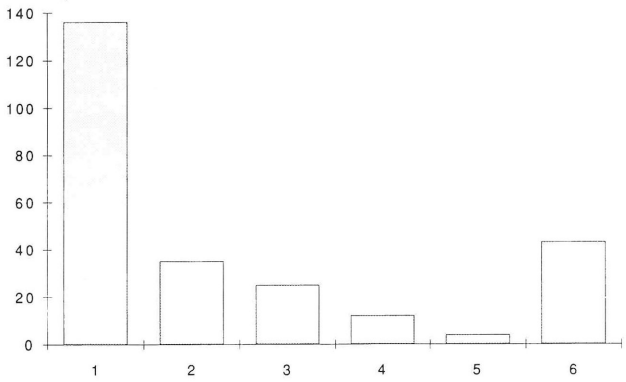
Tab. 1 - Examples of initial basal attachment within free corals.

the contrary, considered the Discocyclinae to act as bioclasts which the corals settle upon. Russo (1979; *in* Carbone *et al.*, 1980) found *Funginellastraea heberti* Tournouer and *Cyclolitopsis patera* Reuss from the Eocene of Capo Mortola (Western Liguria), and Possagno (Treviso, Northern Italy), the first being attached on Operculinae, the second on Discocyclinae. The presence of these two associations is correlated with sedimentological characters. *Funginellastraea* and Operculinae are present in well sorted medium sand, while *Cyclolitopsis* and Discocyclinae prefer muddy silt. Furthermore, the author hypothized that the non-epithecate and costate *Funginellastraea heberti* was a free-living, mobile coral, while the epithecate *Cyclolitopsis patera* could recover from burial by a combination of distension of the polyp and ciliary and tentacular action.

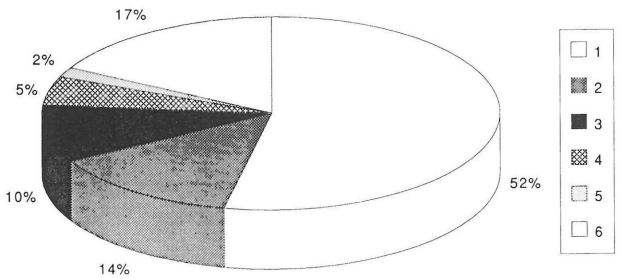
All these associations have been encountered in association with muddy silt and sand substrates.

Small, solitary discoidal, non-epithecate scleractinian corals attached to extraneous objects have been mentioned also from the Cretaceous. De Fromentel (1870) described *Cycloseris provincialis* from the Turonian-Senonian of Le Beausset (France), and Felix (1913) *Cycloseris blanckenhorni* from the Cenomanian of Lebanon.

With regard to *«Cycloseris» escosurae*, we have analyzed two hundred fifty eight specimens. They occur in a packstone with a silt matrix. The clasts are mostly constituted by tests of *Palorbitolina*, associated with reworked shells of fresh or brackish water Conchostraca (genus *?Rhabdostichus* Raymond, 1946), echinoid spines, minute gastropods, Bryozoa, and fragments of bivalves. The associated macrofauna consists of the bivalves *Lopha, Neithea*, teredinids, and gastropods. While substrate selectivity for *Palorbitolina* tests is evident in 136 specimens, a variety of other substrates were utilized by *«Cycloseris» escosurae*, including various bioclasts present on the substrate (Pl. 1 and Pl. 2). In fact, 136



Text-fig. 2 - Histogram for specimens attached on different organisms: 1) *Palorbitolina* tests; 2) bivalve fragments; 3) conchostracan shells; 5) corals and bryozoans; 6) undetermined fragments. Some specimens (column 4) show completely septate basis.

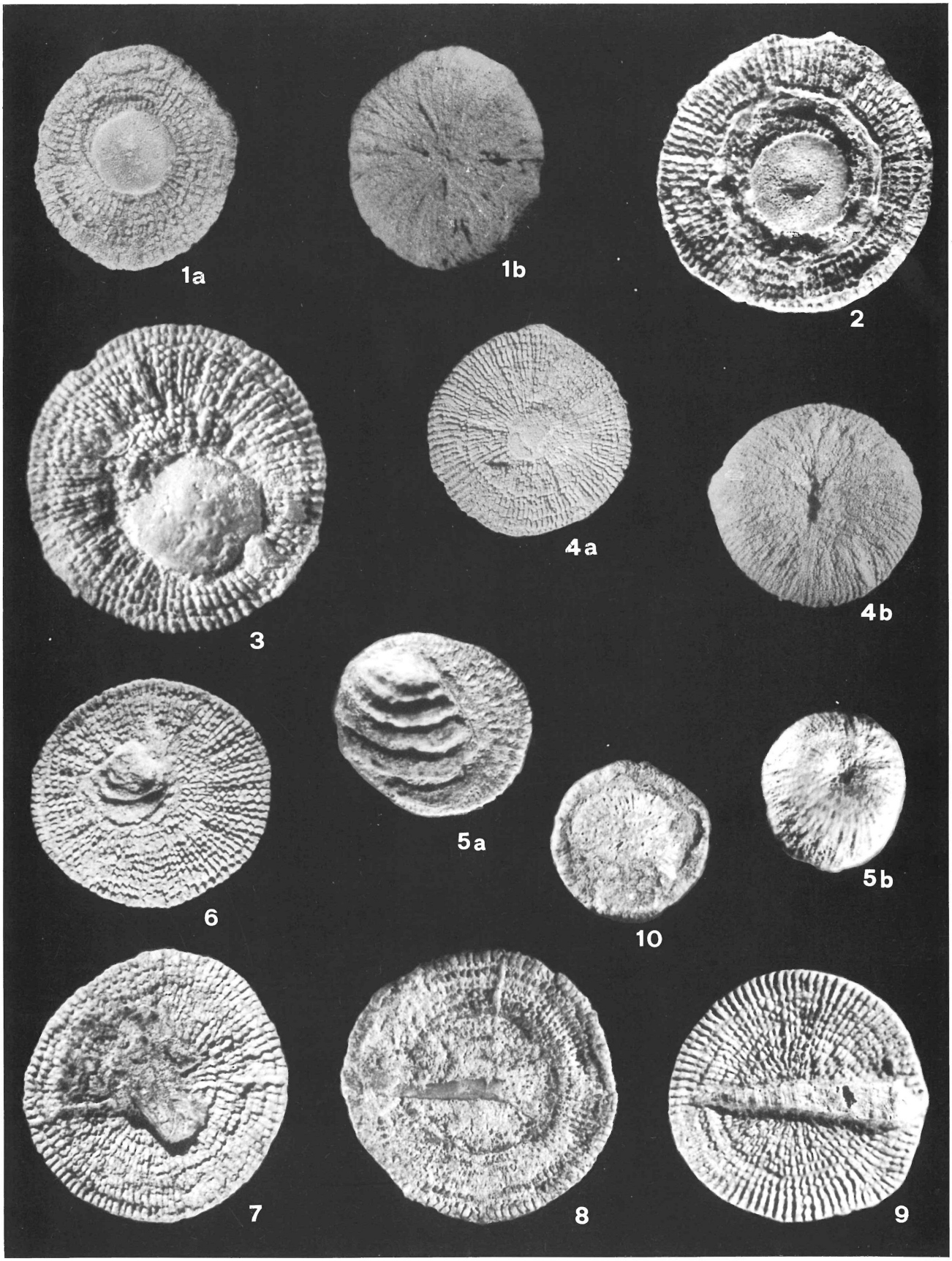


Text-fig. 3 - Pie diagram for % of specimens attached on different organisms: 1) *Palorbitolina* tests; 2) bivalve fragments; 3) conchostracan shells; 5) corals and bryozoans; 6) undetermined fragments. Some specimens (sector 4) show completely septate basis.

specimens (corresponding to 52% of the total) are attached to *Palorbitolina*, 36 specimens (14%) to pieces of bivalves, 25 specimens (10%) to Conchostraca, 4 specimens (about 2%) to very small, juvenile, solitary corals and Bryozoa, 43 specimens (17%) to undetermined bioclastic fragments, and 9 specimens

EXPLANATION OF PLATE 1

Figs. 1-10 - *«Cycloseris» escosurae* Mallada, 1887. Pont de Taules, near Morella (prov. Castellon, Spain).
1a) Aboral view showing the central attachment on *Palorbitolina* test and the lack of epitheca, IPUM no 24939 (x 5); 1b) Oral view of the same specimen (x 5); 2) Aboral view with central *Palorbitolina* test and circular encrustation of worm tube, IPUM no 24940 (x 5); 3) Aboral view with eccentric position of *Palorbitolina* test, IPUM no 24941 (x 5); 4a) Aboral view with a small undetermined bioclast and the costae reaching almost to the centre, IPUM no 24942 (x 5); 4b) Oral view of the same specimen (x 5); 5a) Aboral view; small specimen attached on large and peripheric conchostracan, IPUM no 24943 (x 6); 5b) Oral view of the same specimen (x 5); 6) Aboral view with eccentric concostrachan substrate, IPUM no 24944 (x 5); 7) Aboral view, attachment on bivalve fragment, IPUM no 24945 (x 5); 8) Aboral view, attachment on echinoid spine, IPUM no 24945 (x 5); 9) Aboral view, attachment on turriculate gastropod, IPUM no 24946 (x 5); 10) Aboral view, small specimen attached on bryozoan, IPUM no 24946a (x 6).


1a
1b
2
3
4a
4b
5a
5b
6
10
7
8
9



Text-fig. 4 - Longitudinal polished section showing the attachment to *Palorbitolina* tests, the absence of epitheca and, in some areas, the trabecular trajectories (x 8).

(5%) are free (Text-figs. 2, 3). Only one particular specimen, on which another small solitary coral has settled (Pl. 2, fig. 8), seems to be epithecate, whereas all the others are non-epithecate. Thus, a wide variety of hard particles was used by *«Cycloseris» escosurae*, and the apparent preference for Palorbitolinas was probably due to their dominant abundance and their flattened shape more suitable for larval settlement.

Generally, the position of the coral's attachment upon Palorbitolinas or other shells is central (Pl. 1, figs. 1a, 2), but in some case it is eccentric (Pl. 1, figs. 3, 5, 6). Rarely, in addition to the main object of attachment, there are other small extraneous fragments that are almost completely covered by the septa (Pl. 2, fig. 3), demonstrating that the polyp invested the lower (aboral) side of skeleton and that the growth of the skeleton took place not only upwards and laterally but also downwards. The completely «costate» specimens show also extraneous objects, which are entirely covered by the septa (Pl. 1, fig. 4; Pl. 2, figs. 4, 6a). There are also some substrate particles encrusted by small worms; sometimes the encrusters also extend over the coral, and some worms encrust only the coral (Pl. 1, fig. 2; Pl. 4, fig. 2). These encrustations are present both on the lower and upper sides of the corals. We have not observed a relationship between the size of corals and that of substrate particles. In fact, there are large corals attached on small Palorbitolinas and vice versa.

Dead substrates or symbiosis with living substrates?

As solitary, discoidal corals are often found attached to macroforaminifera, some authors inferred a commensal relationship for such an association.

Among the various types of macrosymbiosis (Lewis, 1985), commensalism applies when one partner benefits and the other neither gains nor loses in fitness, whereas amensalism applies when one partner has no benefits and the other loses in fitness (Darrel & Taylor, 1993).

As it is impossible to obtain fitness data from fossils, Darrell & Taylor (1993) adopt a structural classification of symbioses, independent of the inference of processes such as fitness gains or losses but nevertheless reflecting important aspects of symbiont ecology. They distinguish encrusting, intergrowth and boring categories. Furthermore, there must be evidence that the coral and its associate lived at the same time in order to demonstrate symbiosis and eliminate the possibility of a post-mortem association.

Three principal types of evidence exist for a life association: 1) structures indicating concurrent growth of the coral and its associate, 2) specific orientation of locations of associates, and 3) direct analogy with extant associations known to be symbiotic.

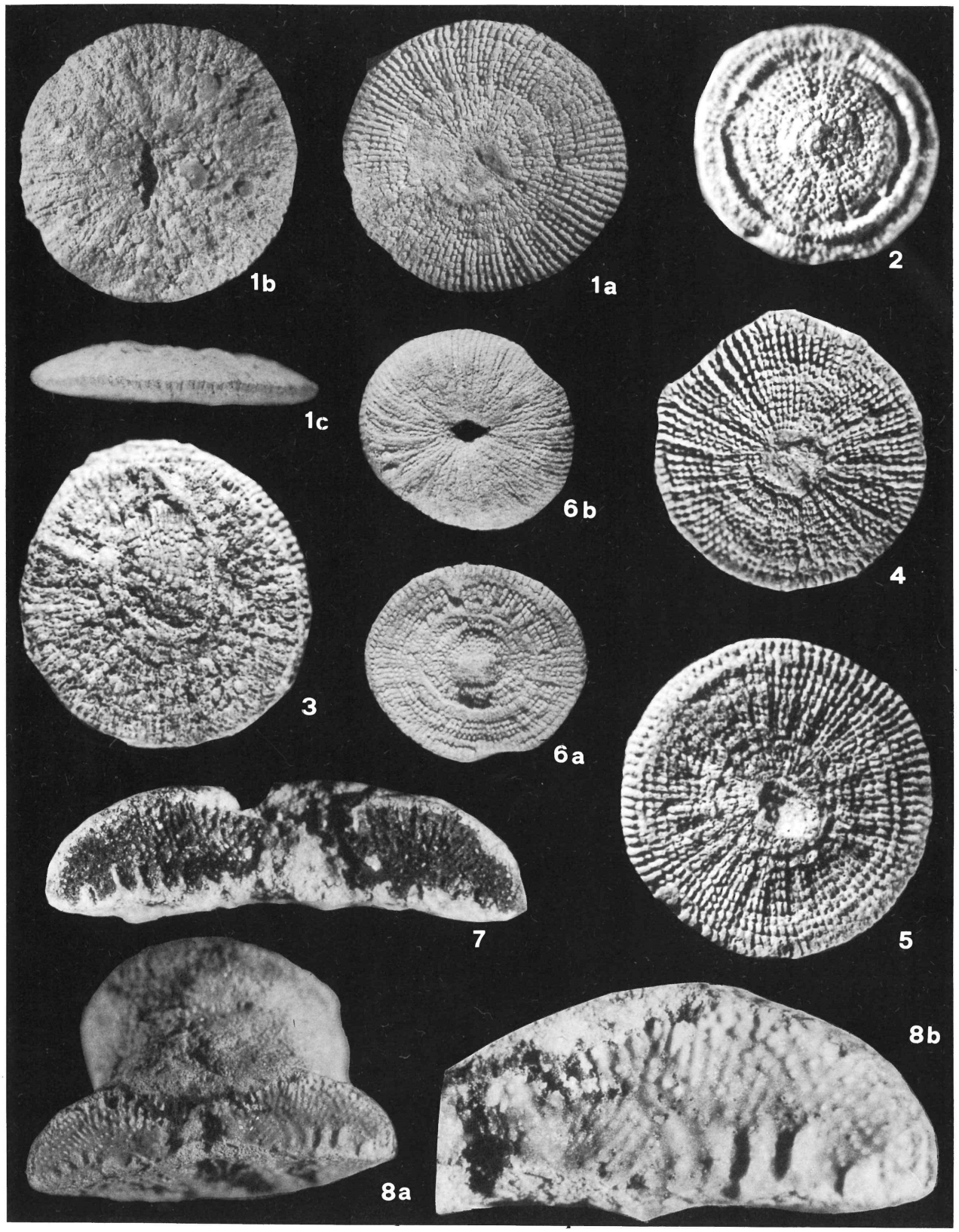
As regards the *«Cycloseris» escosurae* and *Palorbitolina* association, it is hard to find evidence that the coral and its associate lived at the same time. None of the three types of evidence enunciated by Darrell & Taylor (1993) for a life association, can be clearly evaluated.

Structures indicating concurrent growth, such as intimate intergrowths between the coral and the *Palorbitolina* or distinctive growth patterns developed by the *Palorbitolina*, have not been observed. In all the analyzed specimens, the attachment of

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EXPLANATION OF PLATE 2

Figs. 1-8 - *«Cycloseris» escosurae* Mallada, 1887. Pont de Taules, near Morella (Prov. Castellon, Spain).
1a) Aboral view of an entirely septate specimen with the septa reaching the centre, IPUM no 24947 (x 5); 1b) Oral view of the same specimen (x 5); 1c) Lateral view of the same specimen (x 5); 2) Aboral view, attachment of a very small, juvenile solitary coral, IPUM no 24948 (x 5); 3) Aboral view, a probable small bivalve enveloped by the septa, IPUM no 24949 (x 5); 4) Aboral view, undetermined bioclast almost completely enveloped by the septa, IPUM no 24950 (x 5); 5) Aboral view, attachment on conchostracan shell, IPUM no 24951 (x 5); 6a) Aboral view showing a completely septate specimen, IPUM no 24952 (x 5); 6b) Oral view of the same specimen (x 5); 7) Median longitudinal surface showing the fulturae and the disposition of granular ornamentation, IPUM no 24953 (x 12,5); 8a) Median longitudinal surface with fulturae and lateral ornamentation. Note that this specimen is encrusted by an other solitary coral, IPUM no 24954 (x 7); 8b) Enlargement of previous specimen to show the fulturae and ornamentation (x 17).

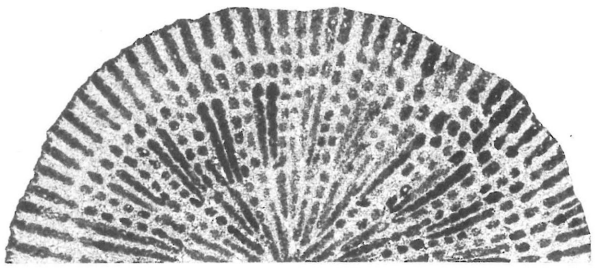

1b
1a
2
1c
6b
4
3
6a
5
7
8b
8a

the coral is direct on the Palorbitolinas, without any secondary «stereom», as found in Devonian and Lower Carboniferous tabulates which encrust crinoids (Hudson *et al.*, 1966; Boucot, 1990). No manifestation could be discerned to the encrusting of the coral upon a living foraminifer.

Finally, from the data at our disposal, we do not know of any direct analogy with extant associations between corals and macroforaminifers, that are symbionts.

On the other hand, there is no clear evidence for post-mortem association, except in few cases where the coral encrusts abraded or broken foraminifers (Pl. 4, fig. 5) and the antapical face of Palorbitolinas. We have analyzed in detail the area of attachment in 20 specimens, in thin sections and on SEM screen. The external foraminiferal wall upon which the coral is attached, does not show marks of microborers, microencrusters, or abrasion (Text-fig. 4; Pl. 4, fig. 3).

In conclusion, there is no evidence supporting a symbiotic association, whereas there is some evidence suggesting post-mortem colonization. Firstly, the coral settled exclusively upon organic «clasts», such as reworked Conchostraca, fragments of bivalves, echinoid spines, etc., consequently post-mortem colonization. This is because the terrigenous clasts are too small (silt to medium sand) to be encrusted by corals. Secondly, the coral became too large and heavy, covering, and in some cases, enveloping completely the foraminifer, which therefore could not have survived in a symbiotic relationship. Thirdly, there are a few examples demonstrating that the coral encrusted eroded and broken *Palorbitolina* tests. From this settlement upon extraneous objects, however, the coral gains the benefit of a hard substrate for larval attachment and avoidance of burial.



Text-fig. 5 - Thin section showing the septal pattern. The transverse bars are the terminations of the vertical bars of fulturae and not dissepiments, (x 8).

Auto-mobility

Gill & Coates (1977) described three different types of coral mobility on soft substrates, each related to a particular skeleton growth and shape. Among these types, they described some corals having an ability for self-induced directional movement that they called auto-mobility. Auto-mobility can be divided into three modes: 1) vertical movement through the sediment to recover from burial, 2) «righting» of the coral after overturning, and 3) migration across the bottom. The last of these is characteristic of corals which generally have in common the complete investiture of the skeleton by the polyp, and therefore cilia on both the oral and aboral surfaces. As most representative of this type of mobility, Gill & Coates have chosen the Recent *Cycloseris cyclolites* Lamarck and the Jurassic *Chomatoseris*.

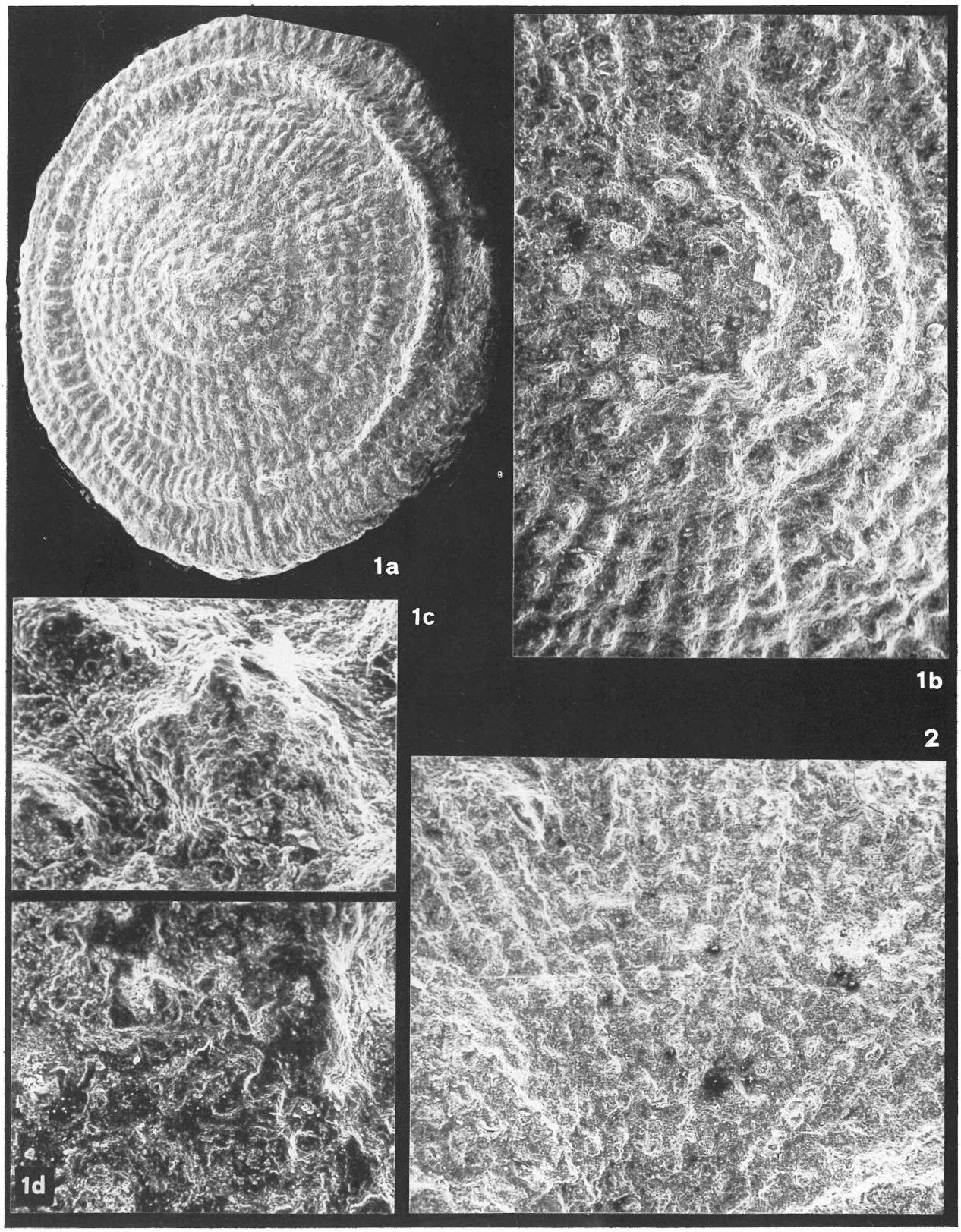
Essential to this third kind of mobility are centrifugal growth through trabeculae directed downwards, and lack of epitheca. The coral must stay small and light, since size and weight rapidly become limiting factors to movement.

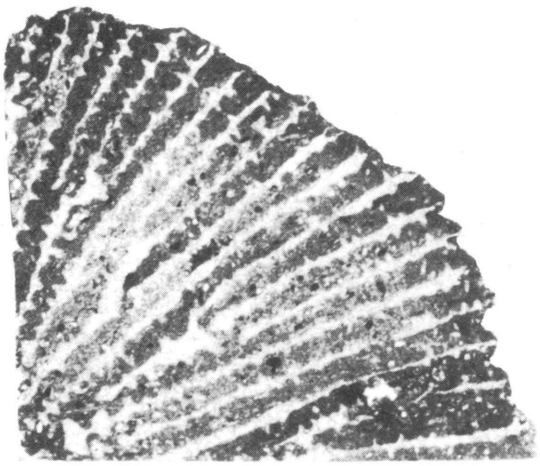
The fossil species *«Cycloseris» escosurae* shows all these characteristics. It is a small, solitary, free coral, although attached in its early stage. The corallum is circular and flattened with a small and suboval deep calicular fossa. Skeletal growth is in all directions, either upwards or downwards (Text-fig. 4). The septa are of montlivaltioid type (Text-fig. 6). Their upper margin shows trifoliate teeth (Pl. 4, fig. 1), as in the family Cyclastraeidae Alloiteau, 1952. Fulturae are present (Pl. 2, figs. 7-8b); dissepiments are absent. There is no epitheca, the lower surface being covered by septa showing trifoliate margins (Pl. 3, fig. 1c), as on the upper surface.

Gill (1970) and Gill & Coates (1977) also described in *Chomatoseris* the presence of extraneous objects, ranging from sand grains to a whole

EXPLANATION OF PLATE 3

Figs. 1a-2 - *«Cycloseris» escosurae* Mallada, 1887. Pont de Taules, near Morella (prov. Castellon, Spain). S.E.M. photographs.
1a) Aboral view of an almost completely costate specimen, IPUM no 24955 (x 13); 1b) Detail of central part, showing the undetermined fragment almost completely covered by septa (x 30); 1c) Detail of trifoliate tooth of aboral septa (x 195); 1d) Detail of terminal edges of aboral septa upon the substrate (x 120); 2) Oral view of an other specimen showing the upper septal margin denticulations, IPUM no 24956 (x 25).


1a
1b
1c
1d
2



Text-fig. 6 - Polished section showing the «montlivaltioid» type of the septa (x 15).

nerineid shell, used for initial attachment, completely enveloped by the skeleton. In our species these objects, which may vary from bivalve fragments to *Palorbitolina* tests, can either be completely enveloped by septa or merely surrounded by them (Pl. 2, fig. 6a).

«Cycloseris» escosurae, therefore, possesses all the main skeletal features associated with mobility that are evident in *Cycloseris* and *Chomatoseris*, namely, small size, basal growth and lack of epitheca.

In what regards the substrate, there is a strong similarity between the substrates preferred by the modern and fossil auto-mobile corals described by Gill & Coates (1977) and those inhabited by *«Cycloseris» escosurae*. In fact, the rock which bears Mallada's species is an *Palorbitolina* packstone-wackestone with interstitial matrix of silt to fine sand-size terrigenous clasts (Pl. 4, fig. 6). Other bioclasts present are fragments of bivalves, small gastropods, echinoid spines, and some Conchostracan tests.

SYSTEMATIC APPENDIX

«CYCLOSERIS» ESCOSURAE Mallada, 1887

1887 *Cycloseris Escosurae* MALLADA, p. 167, pl. 61, figs. 5-8.
1914 *Cycloseris Escosurae* - FELIX, p. 44.
1937 *Cycloseris Escosurae* - BATALLER, p. 305.
1950 *Cycloseris Escosurae* - BATALLER, p. 189.
1952 *Cycloseris Escosurae* - BATALLER, p. 92.

Material - 256 specimens from Early Aptian beds, Pont de Taules, near Morella (Prov. Castellon, Spain).

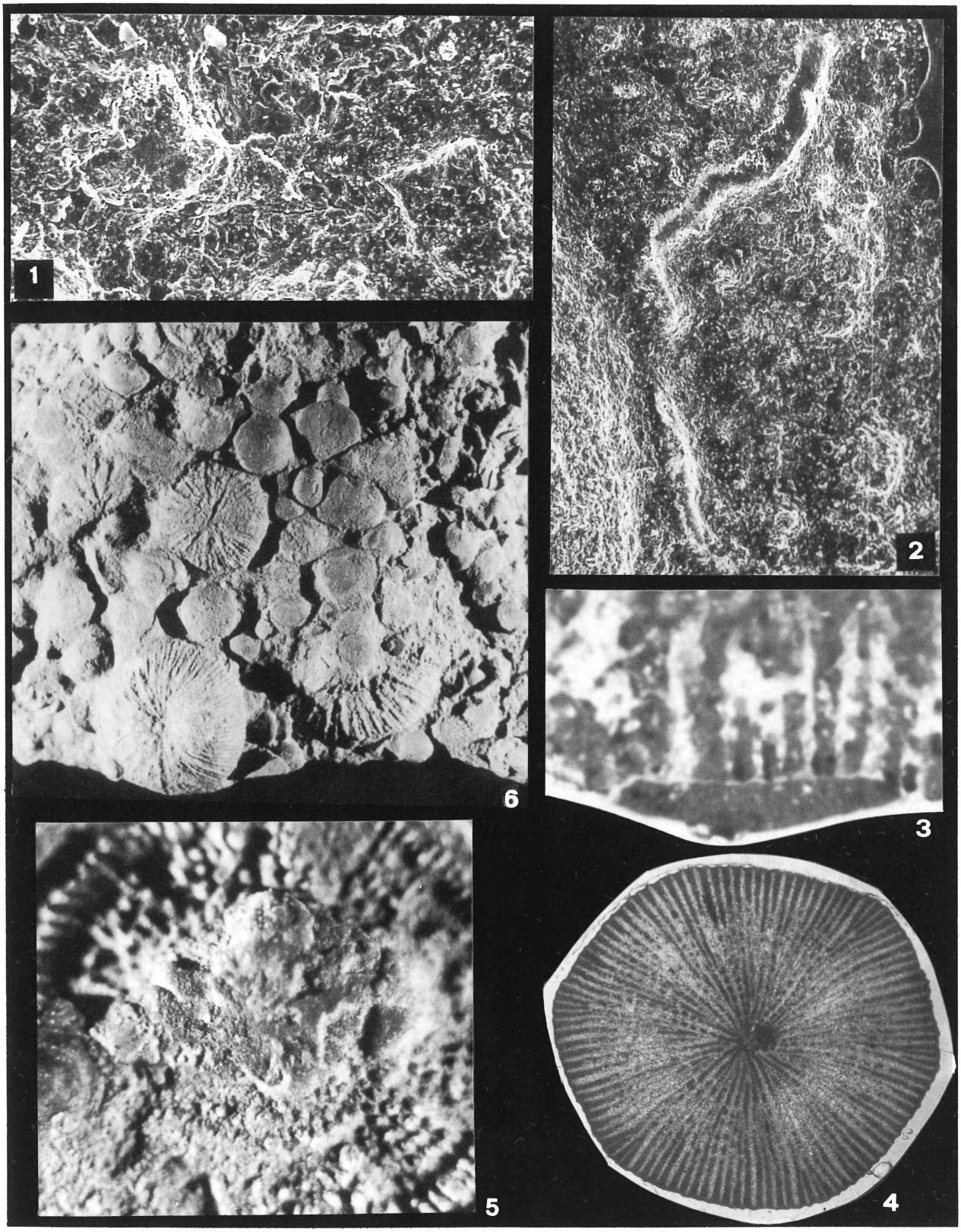
Size - Diameter = 6-18 mm; thickness = 1.5-3 mm.

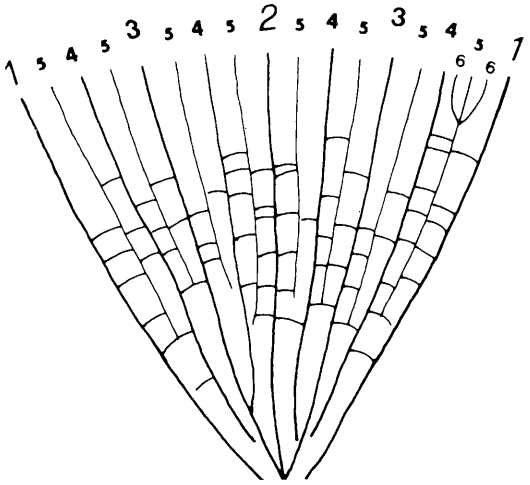
Repository - Institute of Paleontology, Modena University (IPUM), Cat. no. 24939-24961. The catologue numbers for figured specimens are indicated in the plate explanations.

Description - Small, discoidal, solitary, non-epithecate coral. The coral is attached by its lower surface to *Palorbitolina* tests, small fragments of bivalves, small turriculate gastropods, Conchostracan tests, etc. Generally the septa do not cover these extraneous objects, but in few specimens they are completely enveloped by septa (Pl. 2, figs. 1a, 4). The calicular surface is flat or feebly convex; the lower surface can be slightly concave. The coral is circular in outline with a deep calicular fossa, where the more diverging trabeculae simulate a pseudo-papillate columella (Text-fig. 4). The number of septa is around 106, arranged in five complete cycles and the sixth rather incomplete. They are set in six symmetrical sectors (Pl. 4, fig. 4). The pattern of septal arrangement is shown in Text-figs. 5, 7. The upper edges of septa, when well preserved, show trifoliate teeth (Pl. 4, fig. 1); the lateral surface bears small, rounded granules aligned with trabecular trajectories (Pl. 2, figs. 7, 8). The septa are compact and similar to the «montlivaltioid» type of Gill &

EXPLANATION OF PLATE 4

Figs. 1-6 - *«Cycloseris» escosurae* Mallada, 1887. Pont de Taules, near Morella (prov. Castellon, Spain)
1) S.E.M. photograph of a detail of Pl. 3, fig. 2, showing two trifoliate teeth of upper septal margins, similar to those of aboral margin of septa (x 195); 2) S.E.M. photograph of tube worm encrustation on aboral side; on the left the border of *Palorbitolina* test is visible, IPUM no 24957 (x 75); 3) Median longitudinal thin section through the coral and *Palorbitolina* to show the attachment of aboral septa to the foraminifer. The aboral septa are directly attached to the test, IPUM no 24958 (x 25); 4) Thin section showing the septal pattern. The transverse bars are the terminations of the vertical bars of fulturae and not dissepiments, IPUM no 24959 (x 4); 5) Substrate attachment consists of a broken and abraded *Palorbitolina* test, showing that the attachment is subsequent to its abrasion and breakage, IPUM no 24960 (x 25); 6) Rock sample showing the great abundance of *Palorbitolina*, acting as substrate for the corals. Note the abundance of *«Cycloseris» escosurae* specimens, IPUM no. 24962 (x 6).


1
2
6
3
5
4



Text-fig. 7 - Septal pattern of «*Cycloseris*» *escosurae* in one of the six sectors.

Lafuste, 1971 (Text-fig. 6). Fulturae present, consisting of bar-like buttresses.

Dissepiments lacking. The fulturae, the oldest described up to now, are located on major septa (Text-fig. 5), and their height is limited to the basal part (Pl. 2, figs. 7-8b). There is no wall or epitheca, and the lower surface is covered by trifoliate septa (Pl. 3, fig. 1c). The growth of the skeleton is centrifugal, with the trabeculae directed also towards the base, as in *Cycloseris*.

Remarks - Mallada's species shows septal pattern similar that described by Alloiteau (1957) for the genus *Cyclophyllopsis*. From the type-species, *Cyclophyllopsis aptiensis* (de Fromentel, 1870), Aptien of Perte du Rhone (France) it is distinguished mainly by fewer septa (48 septa in de Fromentel's species) and perhaps by the presence of a papillar columella. The septal margin of *Cyclophyllopsis* is indicated as «moniliforme» by Alloiteau, whereas it is «trifoliate» in the Spanish species. From *Cycloseris* Lamarck, the most distinguished characters are the different septal arrangement (see Gill, 1980 for *Cycloseris* septal pattern) and the pattern of fulturae. Remarkable similarities exist also with the genus *Protocycloseris* Russo, 1979, from which the Spanish species differs for fewer septa and fulturae (slender, curved and higher in *Protocycloseris*; stout, stocky, almost erect and shorter in the Spanish species). Further investigations are necessary, both on Mallada and Alloiteau materials, to justify the creation of a new genus.

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