Palaeoecological significance of coral-encrusting foraminiferan associations: A case-study from the Upper Eocene of northern Italy

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Encrusting foraminiferans, although representing an important component of the so-called cryptic assemblages in both modern and ancient reef environments, are in general poorly described and little is known as regards their association with corals. In this paper, we describe coral-encrusting foraminiferan associations in the different facies that characterize the shallowing upward parasequences of the Nago Limestone (Upper Eocene, Trentino, northern Italy). From a relatively deep reef slope up to the shallow shelf-edge, corals have been recognized to be encrusted by different types of foraminiferan assemblages that differ on the basis of relative abundance of species, growth form and type of encrusted coral surface. The succession of encrusting foraminiferan assemblages is interpreted as controlled mainly by light, competition with coralline algae, hydrodynamic energy, and coral growth fabric.

Key words: Encrusting foraminiferans, corals, palaeoecology, reefs, Eocene, Italy.

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Introduction

Within the complex structure of both modern and ancient reefs, encrusting foraminiferans are generally considered as secondary encrusters or binding organisms of minor importance preferentially inhabiting cryptic habitats (lower surfaces of corals and coral rubble, cavities etc.). If particularly abundant, they can be locally important binding organisms, encrusting the primary reef-building community, or even becoming reef builders themselves (Ginsburg and Schroeder 1973; Fagerstrom 1987; Perrin 1987, 1992; Plaziat and Perrin 1992).

Most probably because of their secondary role within reef building processes, and their complex taxonomic identification, encrusting foraminiferans in present-day reefs have been in general poorly described (Brasier 1975; Hottinger 1983; Reiss and Hottinger 1984; Palmieri and Jell 1985; Dullo et al. 1990; Jones and Hunter 1991; Martindale 1992; Reitner 1993; Burch and Burch 1995; Rasser and Piller 1997) and little is known about their relationship with corals. In addition, only a few papers have been published concerning their palaeoecological significance within ancient reef settings (Ghose 1977; Martindale 1992; Perrin 1992; Franquès i Faixa 1996; Matteucci 1996).

In this paper, corals and their encrusting foraminiferans are described in detail within the reef facies of the Upper Eocene Nago Limestone (northern Italy). The shallowing upward succession that characterizes the well exposed type-section of the Nago Limestone is particularly suitable for such a detailed study because it has already been investigated with regard to both its sedimentological and palaeoecological aspects (Luciani et al. 1988; Bassi 1998; Bosellini 1998). It also provides the opportunity to document changes in the main features that characterize the coral-encrusting foraminiferan association along a palaeobathymetric gradient and to establish whether encrusting foraminiferan assemblages can be used as ecological indicators in fossil reef reconstructions.

Geological setting and previous studies

The Nago Limestone is a Middle *pro parte*–Upper Eocene carbonate platform that developed along the western margin of a major Tertiary palaeogeographic element of the Southern Alps known as the Lessini Shelf (Bosellini 1989) (Fig. 1A). Its type section, thoroughly investigated in recent years, is located in the proximity of the homonymous village, at the northeastern corner of Lake Garda in northern Italy (Fig. 1B).

Luciani et al. (1988) recognized the Nago Limestone as being constituted of two major thickening-coarsening-upwards cycles, 42 m and 112 m thick respectively, divided in turn into

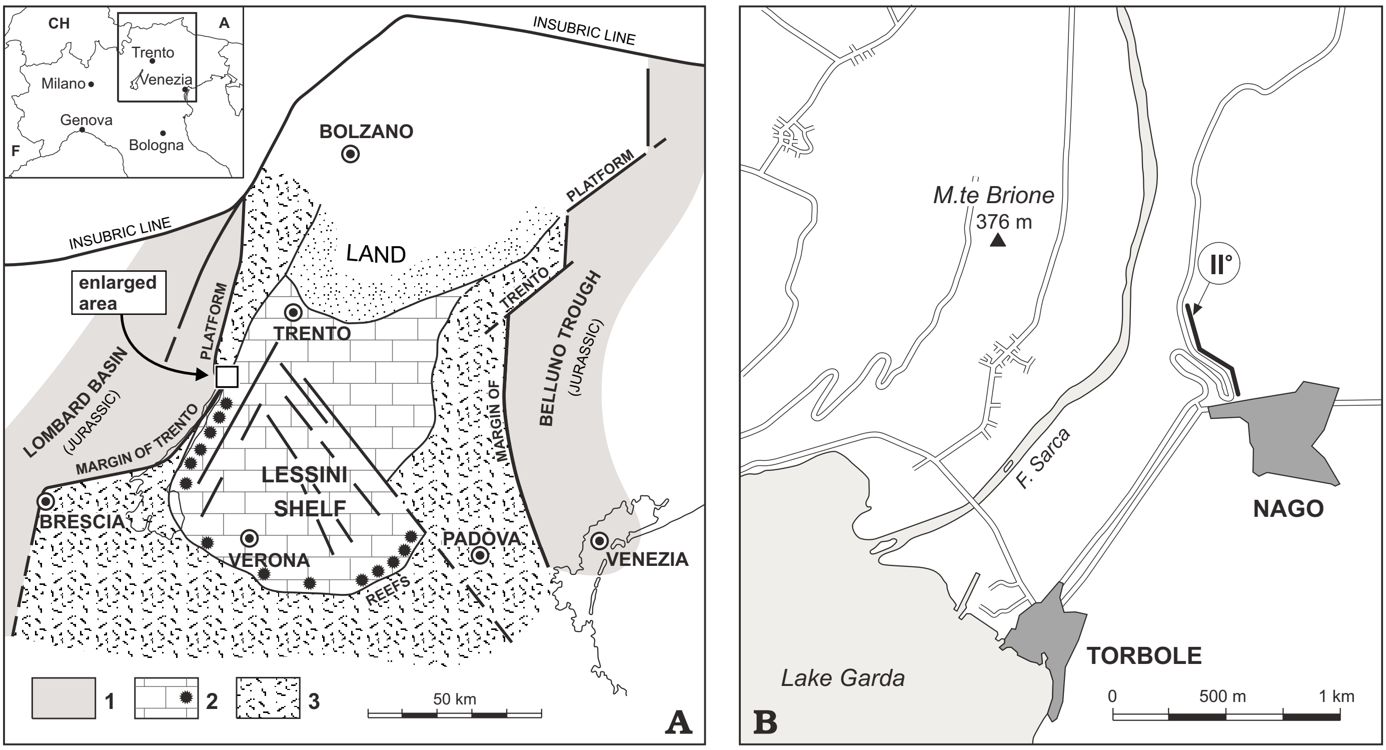

Fig. 1. **A**. Palaeogeographic reconstruction of the Lessini Shelf: 1) deep-water mudstones of the surrounding Jurassic basins; 2) Palaeogene lagoon and shelf-edge reefs; 3) Palaeogene pelagic claystones and marlstones (modified from Bosellini 1989). **B**. Location map of the study area with indication of the Nago Limestone type section (II° major cycle) (from Bosellini 1998).

several minor cycles (Fig. 2A). These are shallowing-upwards parasequences consisting of four facies types, ranging from deep fore-reef to very shallow reef front environments. The facies sets represent repeated progradations of bioclastic-reefal margin deposits towards the basin (Fig. 2B).

The age of the Nago Limestone has been mainly determined according to the larger foraminiferan assemblages, especially *Nummulites*. In particular, the first cycle has been ascribed to the late Middle Eocene, while the assemblage recognized in the second cycle has been considered typical of the Late Eocene (Priabonian), containing among others: *Nummulites fabianii*, *N. incrassatus*, *N. variolarius*, *N. stellatus*, *N. chavannesi*, *Pellatispira madaraszi*, and *Discocyclina sella* (Luciani et al. 1988; Papazzoni and Sirotti 1995). Planktonic foraminiferans and ostracods, also recognized in the marly layers at the base of the second cycle, confirmed a Priabonian age.

Bosellini (1998) recognized the Nago Limestone as being characterized by scattered shelf-edge patch reefs and coral facies have been described and interpreted. Briefly, from the base to the top of the shallowing upward parasequence, the reef slope was characterized by scanty platy corals within the basal and deepest marly facies (Facies 1) and by discontinuous and relatively thin constratal platestones, in association with abundant coralline algae and larger foraminiferans, in the next, relatively less deep facies (Facies 2). At shallower depth, the shelf-edge was characterized by coral patches represented by the thick coral limestone beds of Facies 3 and fringed by the contemporaneous bioclastic sand of Facies 4 (Fig. 2B). The palaeoecological study of Bosellini (1998) also revealed that corals changed with depth in taxonomic composition, in percentage and proportion within the framework and in growth form, allowing the definition of a relative depth coral zonation.

Recently, the type section of the Nago Limestone has also been studied with respect to taxonomy and palaeoecology of coralline algae (Bassi 1998). Some data from this study will be included in the present paper mainly for comparison with encrusting foraminiferans as regards relative abundance and distribution.

Materials and methods

In order to study the association of corals with their encrusting foraminiferans, the three coral-bearing facies of the Nago Limestone shallowing-upward parasequence (Facies 1, Facies 2, and Facies 3) have been analyzed in detail. New data are here provided together with information taken from previous studies (especially Bosellini 1998). Coral facies are described on the basis of macroscopic observations and microfacies analysis. For each facies, data about corals and encrusting foraminiferans, and information about the intra-reef sediment and associated fauna are given.

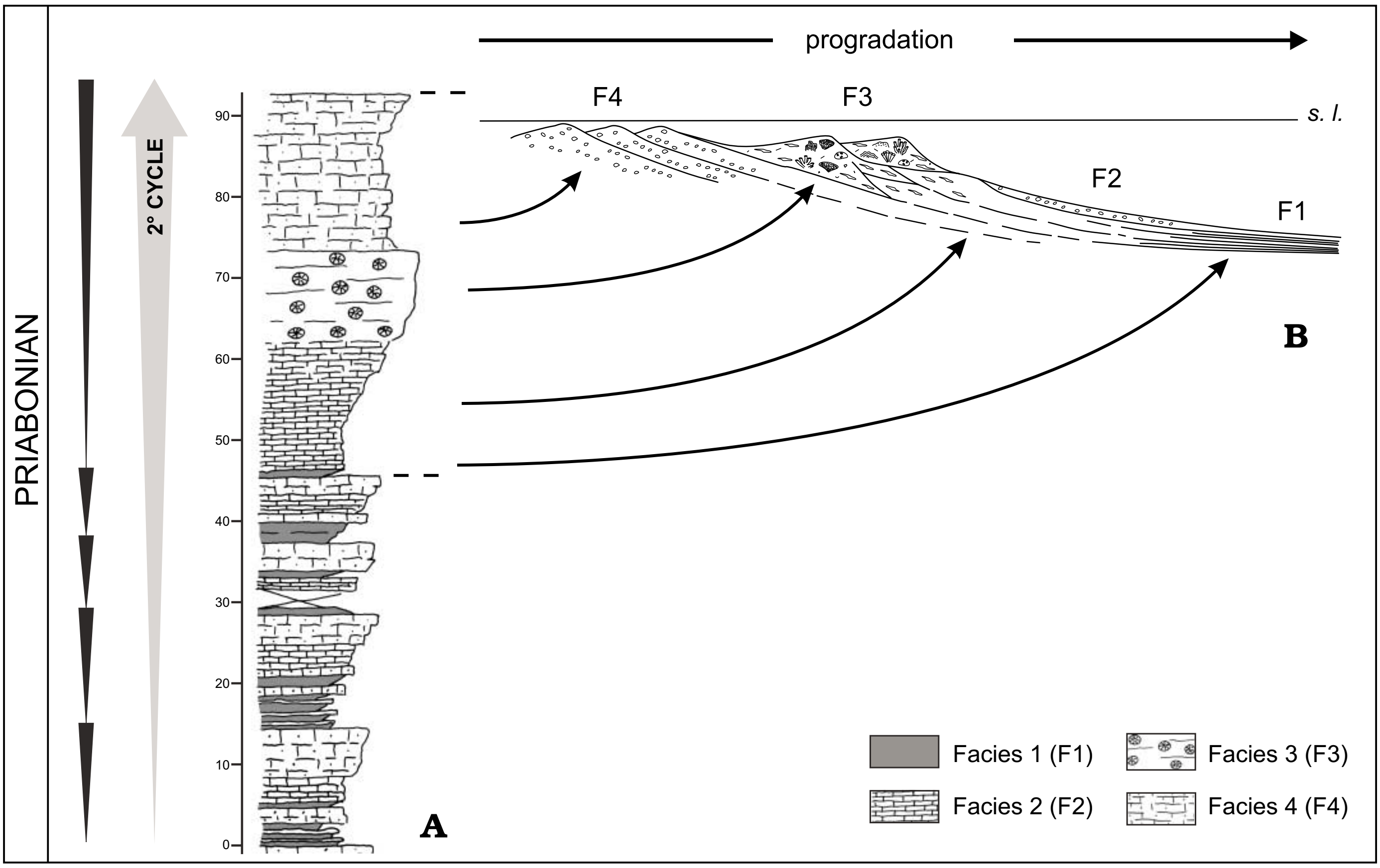

Fig. 2. **A**. The portion of the Nago Limestone type section corresponding to the second major cycle. Minor cycles and facies types are also indicated (from Bosellini 1998). **B**. Model of the uppermost shallowing-upward parasequence showing distribution of facies types along the Nago Limestone shelf-edge.

For corals, taxonomic identification is provided together with relative abundance and detailed descriptions of their growth form. Data also include quantitative estimation of the framework density and identification of growth fabric, according to the recent terminology proposed by Insalaco (1998).

For the study of encrusting foraminiferans, 23 coral colonies in growth position have been collected within the three coral-bearing facies. For each colony, orientation has been marked and several thin sections made on their upper and lower surfaces (Table 1). For each thin section, the following features were considered: 1) taxonomic identification of the encrusting foraminiferans; 2) number of individuals; 3) encrusted coral surface (upper and lower surface of corals); 4) growth morphology; 5) association with encrusting coralline algae (foralgal crusts); and 6) notes about other peculiar characters.

Identification of growth morphology was undoubtedly biased by the two-dimensional observation of the foraminiferans in thin section. However, two main morphotypes have been distinguished on the basis of the prevalent direction of growth: flat (prevalent horizontal growth) and globose (prevalent vertical growth) (Martindale 1992; Elliott et al. 1996).

Within thin sections, the encrusting foraminiferans found in the matrix (free or associated with algal crusts or rhodoliths) have also been considered. In total, 64 thin sections were analyzed (13 for Facies 1, 30 for Facies 2, and 21 for Facies 3) and more than 390 specimens of encrusting foraminiferans were examined. In order to obtain homogeneous data, the percentage of all taxa in the total assemblage has been calculated for each facies. Also, for each facies, the following quantitative data are provided: a) the percentages of the different groups of Foraminifera (i.e., families–suborders); b) the percentages of isolated encrusting specimens *versus* foralgal crusts and their preferential attachment surface; and c) the percentages of globose *versus* flat morphotypes.

However, dealing with relatively big differences in sample size (i.e., number of thin sections per facies), a statistical analysis has been considered necessary in order to reduce bias in the non-normally-distributed data set. Data were analyzed by means of SPSS 10.0 Statistical Package (SPSS, Chicago, IL, USA). The occurrence of each encrusting foraminiferan species within each facies was expressed by mean ±SD. Data were first analyzed via non-parametric ANOVA (Kruskal-Wallis). Post hoc analyses were performed via Mann-Whitney U test. Statistical significance was set at $p < 0.05$.

Finally, a taxonomic list of the encrusting foraminiferans recognized in the Nago section is included at the end of the paper (Appendix). The classification mainly follows Loeblich and Tappan (1987) and, for the acervulinids, Perrin (1994).

Table 1. List of coral samples collected in Facies 1, Facies 2, and Facies 3. For each coral sample, coral taxon, the number of thin sections and their position with respect to coral lower and upper surface are indicated.

	Sample	Coral taxon	no. thin sections	no. upper surfaces	no. lower surfaces
Facies 1	N5	*Cyathoseris* sp.	3	2	1
	N6	*Cyathoseris* sp.	4	2	2
	N9	*Cyathoseris* sp.	3	2	1
	N15	*Cyathoseris* sp.	3	2	1
	N1	*Actinacis rollei*	3	1	3
	N2	*Actinacis rollei*	11	7	4
	N3	*Actinacis rollei*	4	0	4
	N4	*Actinacis rollei*	2	0	2
Facies 2	N11	*Actinacis rollei*	4	1	3
	N13	*Actinacis rollei*	2	1	0
	NB3	*Actinacis rollei*	1	1	1
	NB5	*Cyathoseris* sp.	2	1	1
	SNA2	*Actinacis rollei*	1	1	0
	N7	*Actinacis rollei*	4	3	1
	N16	*Goniopora* sp.	2	1	1
	N8	*Acropora* sp.	1	1	0
	N14	*Actinacis rollei*	2	1	1
Facies 3	N24	*Actinacis rollei*	2	1	1
	N10	*Antiguastrea lucasiana*	1	1	0
	N20	*Astreopora tecta*	2	2	0
	N18	*Actinacis rollei*	1	0	1
	N23	*Actinacis rollei*	3	2	1
	N16	*Actinacis rollei*	3	2	1

The thin sections described in this paper are housed at the Dipartimento del Museo di Paleobiologia e dell'Orto Botanico in Modena (former Istituto di Paleontologia dell'Università di Modena, abbreviated IPUM).

Coral facies

Descriptions of coral facies have been here divided into three parts. The first one includes general aspects like main lithology, type of sediment and other outcrop macroscopic features, together with information about the associated fauna (all the fauna occurring within the reef excluding the corals and encrusting foraminiferans). The second and third parts are dedicated to the description of corals and encrusting foraminiferans, respectively.

Facies 1

General aspects.—This facies is represented by marly limestones and marls, in slightly nodular beds; thickness is about 2 m. Limestones are bioturbated, poorly sorted wackestones, occasionally wackestone-packstone, with abundant coralline algae, associated with larger foraminiferans. Alternating beds of 5–10 cm thick wackestones are clearly visible and appear to be dominated by rhodoliths and coralline crusts. Corals are rare.

The associated fauna consists of coralline algae (dominant algal genera in order of importance: *Mesophyllum*, *Sporolithon*, *Lithothamnion*, *Lithoporella*, according to Bassi 1998), larger foraminiferans (*Nummulites*, *Discocyclina*, *Asterocyclina*, *Assilina*, *Heterostegina*, *Asterigerina*) associated with some planktic foraminiferans, echinoids, small thin bivalves, some pectinids, large ostreid bivalves (cf. *Pycnodonta*), serpulids, bryozoans, ostracods.

Corals.— Corals are rare, and when present are grouped in 2–4 colonies that are represented by only one genus: *Cyathoseris*. The very low abundance and diversity of corals prevented identification of a clear growth fabric for this facies and no quantitative measurements have been applied. Colonies of *Cyathoseris* show a clear platy growth form according to Rosen et al. (2002) where platy morphotypes are defined as thin, flat unifacial coral colonies, with broadly upward-facing calical surfaces, and the dominant orientation of plates is more or less horizontal and lying parallel to bedding. Platy *Cyathoseris* are here not very well developed in size (about 40 mm large and 5–7 mm thick). They may develop superstratal laminae, as documented by their lower surfaces colonized by cryptic encrusters (some serpulids have been observed along with foraminiferans), or rest directly on the substrate. Some colonies are bored by lithophagids. Upper surfaces of corals are commonly encrusted by thin algal crusts and foraminiferans.

Encrusting foraminiferans.—In this facies, encrusting foraminiferans are in general not very frequent. On average, three specimens have been recorded in each thin section. About fourteen taxa have been identified, but only nine were found attached to the coral surfaces. The relative abundance of taxa is indicated in Fig. 3.

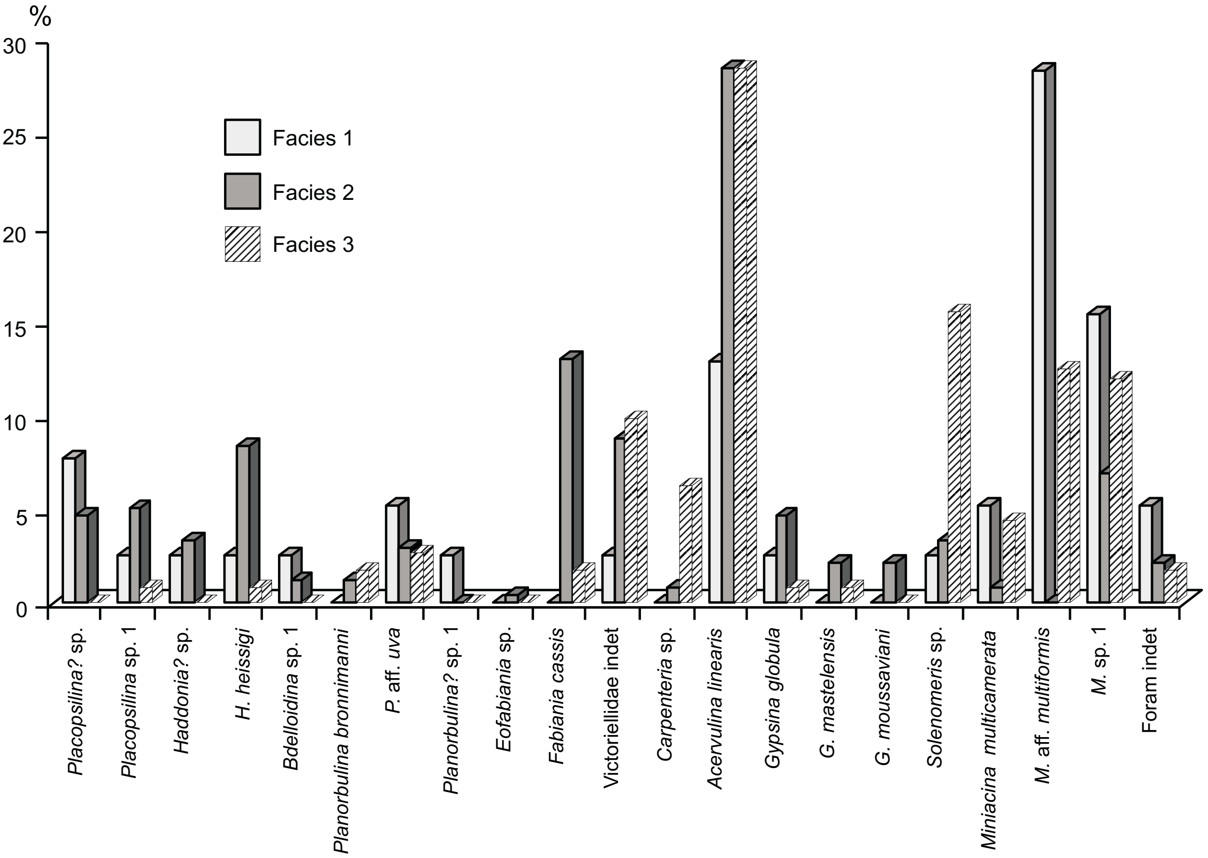

Fig. 3. Encrusting foraminiferans recognized in the Nago section and their relative abundance within Facies 1, Facies 2, and Facies 3.

The Homotrematidae of the genus *Miniacina* (*M.* aff. *multiformis* and *M.* sp. 1; flat morphotypes) represent about 50% of the assemblage (Fig. 4A). *Miniacina* aff. *multiformis* (28%) shows no preferential attachment surface (Fig. 5A), whereas *M.* sp. 1 (15%) seems to encrust the lower surfaces of corals (Fig. 5B). Subordinately, the Textulariina and Acervulinidae represent 19% of the assemblage each (Fig. 4A). Textulariina belonging to the genus *Placopsilina* (10%) encrust the upper surface of corals developing a globose morphology (Fig. 5A). The Acervulinidae are mostly represented by *Acervulina linearis* (13%), although it occurs within the matrix and is never found attached to the corals.

In this facies, foraminiferans equally encrust both upper and lower surfaces of corals, with about the same number of individuals. However, it has been observed that whereas on upper surfaces they are nearly always associated with coralline algae to form thin foralgal crusts, on lower surfaces they usually occur as isolated encrusting specimens (Fig. 6). Algal crusts are very rare on coral lower surfaces.

Facies 2

General aspects.—This facies, 15–16 m thick, consists of thin beds (10–20 cm) of a grey wackestone/packstone rich in coralline algae, larger foraminiferans and platy corals. Platy corals occur within scattered horizons that commonly overlie algal crust-bearing beds. Rhodolith floatstones are common on the top of the coral horizons where they form extensive layers (Bassi 1998).

Coralline algae are mainly represented by crusts and rhodoliths and, according to Bassi (1998), the dominant genera are in order of importance: *Sporolithon*, *Mesophyllum*, *Lithothamnion* and *Lithoporella*. The larger foraminiferan association is mainly characterized by *Discocyclina*, *Assilina*, *Heterostegina*, *Asterigerina*, *Asterocyclina*, *Nummulites* (*N. fabianii*, *N. incrassatus*), and *Spiroclypeus*. Other associated organisms are represented by gastropods, bivalves (some pectinids, large ostreids, lithophagids), echinoids, bryozoans and serpulids.

Corals.—Following the terms recently introduced by Insalaco (1998), the growth fabric of this coral assemblage should be designated as a constratal loose platestone-sheetstone, uniform and discontinuous. An average coral cover of about 15% has been estimated by the measurement of two transect lines (Bosellini 1998). A low coral diversity has been observed, dominated by the species *Actinacis rollei* and, secondly, by *Cyathoseris* sp. (*Actinacis rollei–Cyathoseris* association of Bosellini 1998). One or two colonies of *Colpophyllia* sp. have been observed. All corals show, in general, a rather platy growth form.

Within the coral beds of Facies 2, some changes have been observed from the base towards the top. Corals at the

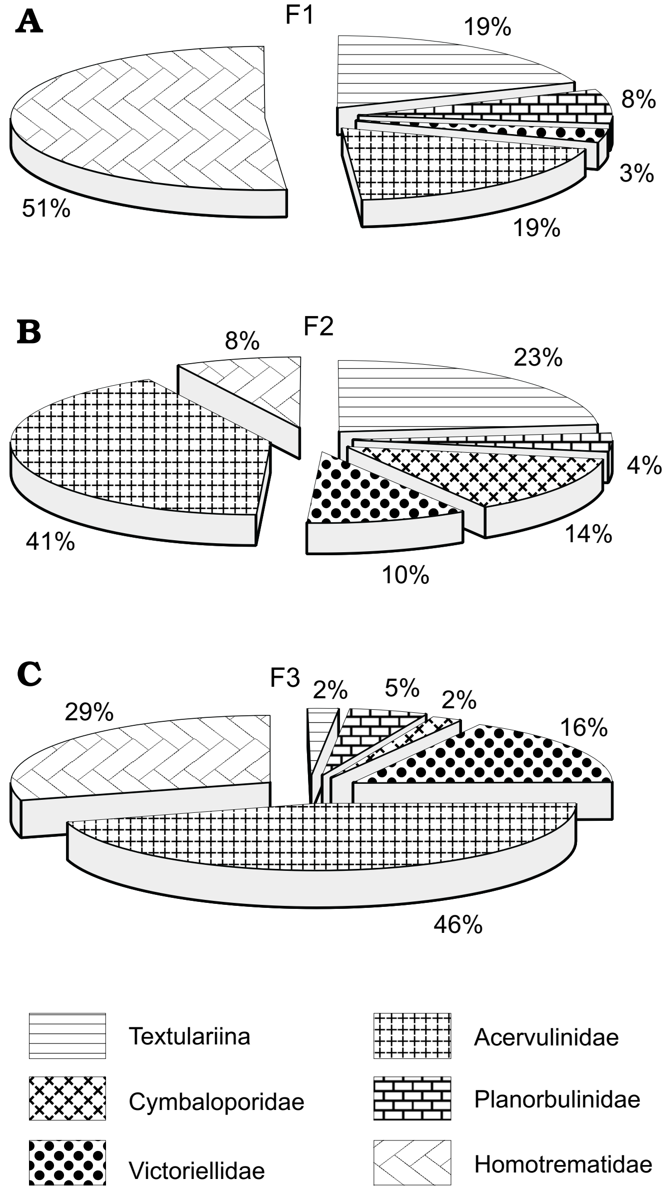

Fig. 4. Relative abundance of the different groups of encrusting foraminiferans (families and suborders) within Facies 1 (**A**), Facies 2 (**B**), and Facies 3 (**C**).

base are less in number and generally larger with respect to those found at the top (they can reach 0.7–1 m in width), and show a slightly convex upper surface (slightly domal). Some of these corals are "attached" to valves of large ostreids (contacts show dissolution structures). Surfaces of corals are here encrusted by crusts of coralline algae and by encrusting foraminiferans. Their lower surfaces (superstratal laminae that seem to be more or less parallel to bedding/substrate) are usually colonized by cryptic encrusters. Intrareef sediment is here very similar to that of Facies 1, being constituted of a poorly sorted, highly bioturbated wackestone-packstone. Rhodoliths and algal crusts are abundant.

Towards the top, sediment becomes coarser (dense bioclastic packstone), is moderately sorted, has more rounded fragments, is less micritic and less bioturbated. Algal crusts are less common. Corals, namely *A. rollei* and *Cyathoseris,* are relatively more abundant but smaller (about 20–30 cm in diameter). Growth form is strictly platy, with flat colonies lying directly on the substrate. Superstratal laminae are less common and in only one case was a cryptic bryozoan observed encrusting a coral lower surface. Coral upper surfaces are encrusted by coralline algae and often bored by serpulids and lithophagid bivalves.

Encrusting foraminiferans.—This is the facies with the highest number of encrusting species and individuals. In total, eighteen taxa (twelve attached to the corals) have been identified and on average about eight specimens per thin section were counted. The relative abundance of taxa is indicated in Fig. 3.

The Acervulinidae clearly dominate, comprising more than 40% of the specimens (Fig. 4B). In particular, *A. linearis* reaches its maximum abundance in this facies (28%), encrusting both upper and lower surfaces of corals, with a slight preference for the lower surfaces (Fig. 7A, B). The Cymbaloporidae (14%, Fig. 4B), totally absent in the former facies, are mainly represented by relatively abundant flat specimens of *Fabiania cassis* (13%) that seems to prefer the lower surface of corals (Fig. 7C) or some sheltered upper surfaces as well. The second more abundant group is represented by the Textulariina (23%), with flat *Haddonia heissigi* encrusting the lower surfaces of corals (Fig. 7D), and globose specimens of *Placopsilina* usually occurring on the upper surfaces. The Victoriellidae (10%) only encrust the upper surfaces of corals. The Homotrematidae are poorly developed with respect to Facies 1 (8%, Fig. 4B) and are mainly represented by flat morphotypes of *Miniacina* sp. 1, encrusting both upper and lower surfaces of corals, often within algal crusts (Fig. 7E).

In this facies, foralgal crusts are very well developed both on coral upper surfaces and especially, contrarily to Facies 1, also on their lower surfaces (Figs. 6, 7F). As indicated in Fig. 6, about two thirds of the encrusting foraminiferans belong to these crusts in Facies 2.

Facies 3

General aspects.—At the outcrop scale, Facies 3 consists of massive coral beds (total thickness of 12 m) which constitute the top of the escarpment immediately to the north of Nago. Here, facies mapping clearly indicated the occurrence of two distinct coral buildups separated, and partly surrounded, by the bioclastic sand of Facies 4.

Sediment largely consists of packstones and floatstones with locally abundant micritic matrix. Bioclasts are mainly represented by abundant fragments of corals and coralline algae, larger foraminiferans, bryozoans, and echinoids. Coralline algae generally occur as fragments or crusts and are dominated by mastophoroid genera, in contrast with Facies 1 and 2 that are largely dominated by melobesioids and sporolithaceans (Bassi 1998). Dominant genera in order of importance are *Neogoniolithon*, *Spongites*, and *Lithoporella* (Bassi

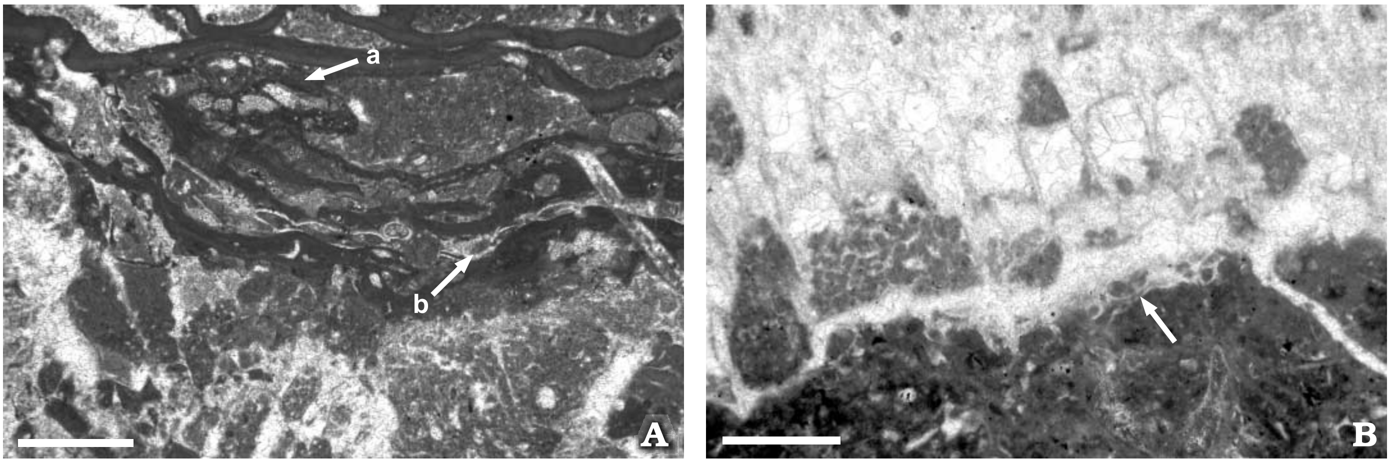

Fig. 5. Encrusting foraminiferans of Facies 1. **A**. IPUM 27825, foralgal crust with *Placopsilina* sp. (a) and *Miniacina* aff. *multiformis* Scheibner, 1968 (b) on the upper surface of the coral *Cyathoseris*. **B**. IPUM 27826, *Miniacina* sp. 1 encrusting the lower surface of the coral *Cyathoseris*. Scale bar 1 mm.

1998). Larger foraminiferans mainly consist of *Nummulites*, *Heterostegina*, *Asterocyclina*, and *Discocyclina*, together with rotaliids and miliolids.

Corals.—Bosellini (1998) recognized a progressive shallowing upward trend in one of the two patches identified within Facies 3. This allowed definition of a relative depth zonation characterized by a *Plocophyllia bartai* association in the deeper part and an *Actinacis rollei* association at shallower depths.

The *Plocophyllia bartai* association is represented by 13 coral species, mainly showing a phaceloid and massive growth form, and is dominated by the phaceloid coral *P. bartai*. Identified corals include the following: *Plocophyllia bartai, Actinacis rollei*, *Leptomussa* sp., *Goniopora rudis*, *Astreopora tecta*, *Stylophora* sp., *Pavona bronni*, *Alveopora rudis*, *Caulastrea fusinieri*, *Montastrea guettardi*, *Antiguastrea lucasiana*, *Cereiphyllia tenuis*, and *Agathiphyllia gregaria*. Growth fabric can be classified as a superstratal sparse pillarstone-mixstone.

The *Actinacis rollei* association is characterized by a decrease in coral diversity (7 coral species have been recognized: *Actinacis rollei*, *Plocophyllia bartai*, *Cereiphyllia tenuis*, *Caulastrea fusinieri*, *Astreopora tecta*, *Goniopora* sp., and *Acropora* sp.) and is dominated by platy-encrusting colonies of *A. rollei*. The growth fabric can be classified as a constratal rigid sheetstone-mixstone, generally discontinuous with an estimated coral cover of about 30–37%. The growth form exhibited by *Actinacis rollei* is chiefly platy with relatively small colonies (about 10–40 cm large and 2–5 cm thick, rarely reaching 10 cm) encrusting the substrate and locally forming dense small patches (Bosellini 1998: fig. 7). Coral upper surfaces are commonly covered by relatively thick algal crusts, as also documented by the quantitative data of Bassi (1998: 184, fig. 6) that show a major abundance of algal crusts within this facies. Generally, corals of this facies are not bored in contrast to those of Facies 2.

Encrusting foraminiferans.—Analogous to Facies 1, fourteen species of encrusting foraminiferans have been identified. However, the number of individuals is higher, with more than five individuals per thin section. Only nine species were found encrusting coral surfaces. The relative abundance of taxa is indicated in Fig. 3.

The assemblage (Fig. 4C) is again characterized by the dominance of the Acervulinidae (46%), but here the distinctive feature is the abundance of *Solenomeris* sp. (16%). There is also a considerable number of Homotrematidae (29%) and Victoriellidae (16%), with a significant occurrence of *Carpenteria* sp. (6%). The Textulariina, relatively abundant in the two previous facies, are here poorly represented (2%).

Foraminiferans encrusting coral lower surfaces are common in this facies but, with respect to Facies 2, they are mainly represented by isolated specimens rather than foralgal crusts (Fig. 6). In particular, flat *Solenomeris* (Fig. 8A) and *Acervulina linearis* dominate the encrusting fauna.

The globose specimens of *Carpenteria* sp. are present both on upper and lower surfaces (Fig. 8B). The upper surfaces of corals are commonly encrusted by flat *Acervulina linearis*, *Miniacina* sp. 1, and Victoriellidae that, subordinately to coralline algae, form quite well-developed foralgal crusts (Figs. 6, 8C, D). Within these crusts also some globose *Haddonia heissigi* and *M.* aff. *multiformis* occur (Fig. 8E, F). *Miniacina* sp. 1, in contrast to Facies 1, encrusts the coral upper surfaces, often with rather flat morphotypes (Fig. 8D).

Encrusting foraminiferan assemblages

Summary of results

Analysis of the taxonomic composition and of relative abundance of species of the encrusting foraminiferan fauna within the three coral facies, has been integrated with a non-para-

Table 2. Occurrence (mean±S.D.) of encrusting foraminiferans within each facies (F1, F2, F3). (a) Facies 2 *versus* Facies 3, $p < 0.05$; (b) Facies 2 *versus* Facies 1, $p < 0.05$; (c) Facies 3 *versus* Facies 1, $p < 0.05$; d) Facies 3 *versus* Facies 2, $p < 0.05$; e) Facies 1 *versus* Facies 2, $p < 0.05$; (Mann-Whitney U test).

Encrusting foraminiferan species	Facies 1	Facies 2	Facies 3
Placopsilina? sp.	0.23±0.59	0.36±0.8 (a)	0±0
Placopsilina sp. 1	0.077±0.27	0.4±0.77 (a,b)	0.047±0.21
Haddonia? sp.	0.077±0.27	0.26±0.52 (a)	0±0
H. heissigi	0.077±0.27	0.66±1.26 (a,b)	0.047±0.21
Bdelloidina sp. 1	0.077±0.27	0.1±0.4	0±0
Planorbulina bronnimanni	0±0	0.1±0.4	0.095±0.3
P. aff. *uva*	0.15±0.37	0.23±0.56	0.14±0.47
Planorbulina? sp. 1	0.077±0.27	0±0	0±0
Eofabiania sp.	0±0	0.033±0.18	0±0
Fabiania cassis	0±0	1.03±1.88 (a,b)	0.095±0.3
Victoriellidae indet	0.077±0.27	0.7±1.02 (b)	0.52±0.74 (c)
Carpenteria sp.	0±0	0.066±0.25	0.33±0.57 (c,d)
Acervulina linearis	0.38±1.12	2.26±2.79 (b)	1.52±1.8 (c)
Gypsina globula	0.077±0.27	0.36±0.99	0.047±0.21
G. mastelensis	0±0	0.16±0.37	0.047±0.21
G. moussaviani	0±0	0.16±0.37 (a)	0±0
Solenomeris sp.	0.077±0.27	0.26±0.58	1.9±5.38 (c,d)
Miniacina multicamerata	0.15±0.37	0.066±0.25	0.23±0.43
M. aff. *multiformis*	0.84±0.8 (e)	0±0	0.66±0.79 (d)
M. sp. 1	0.46±0.96	1.6±6.36	1.71±5.4
Foram indet	0.15±0.37	0.16±0.37	0.095±0.30

metric statistical analysis that compared the occurrence (mean ±SD) of each taxon among the three facies (F1, F2, F3; Table 2). Results underline real differences, and not artifacts of sample size, in the fauna of the three facies allowing recognition of three main assemblages based on distinctive and statistically significant taxa (Table 2).

1) *Miniacina* aff. *multiformis* assemblage (Facies 1). This assemblage is characterized by the dominance of the Homotrematidae with the species *Miniacina* aff. *multiformis* (Table 2) significantly more abundant, especially with respect to Facies 2. This assemblage is also characterized by abundant foralgal crusts on upper surfaces of corals and by isolated encrusting specimens on their lower surfaces, where algal crusts are very rare (Fig. 6). The flat *versus* globose morphotype ratio, as calculated on the whole number of attached specimens, is about 2:1 (Fig. 9).

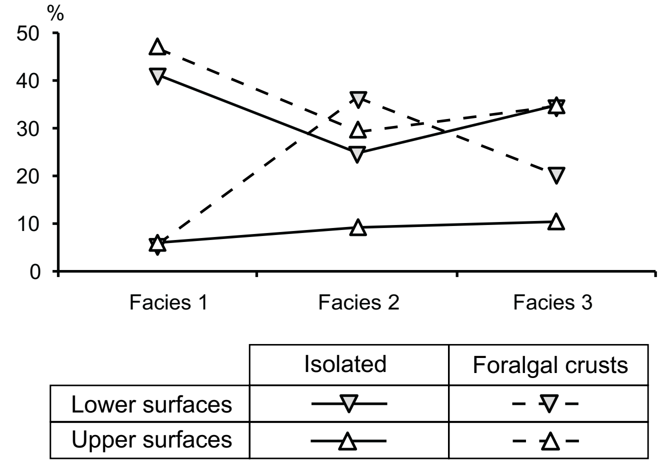

Fig. 6. Diagram showing the percentages of isolated encrusting foraminiferan specimens *versus* foralgal crusts and their preferential attachment surface within Facies 1, Facies 2, and Facies 3.

2) *Acervulina–Fabiania–Haddonia* assemblage (Facies 2). Specimens of *Acervulina linearis* clearly dominate, also with respect to Facies 1 (Table 2). The Cymbaloporidae genus *Fabiania* is also common and characteristic of this facies, being absent in Facies 1 and very rare in Facies 3 (Table 2). The easily recognizable *Haddonia heissigi* is also characteristic. The Homotrematidae, dominant in Facies 1, are poorly represented in Facies 2. In this assemblage, encrusting foraminiferans mainly occur within foralgal crusts, on both upper and lower surfaces of corals (Fig. 6). The flat *versus* globose morphotype ratio is about 3:1 (Fig. 9).

3) *Solenomeris–Carpenteria* assemblage (Facies 3). Here *Solenomeris* sp. and *Carpenteria* sp. appear significantly more abundant with respect to the other facies (Table 2). *A. linearis* is also abundant, although not so much as in Facies 2. Within this assemblage, isolated foraminiferans encrusting coral lower surfaces are equally as developed as those belonging to foralgal crusts on upper surfaces of corals (Fig. 6). The flat *versus* globose morphotype ratio increases to about 5:1 (Fig. 9).

Palaeoecological interpretation

As already observed for corals (Bosellini 1998), encrusting foraminiferans also change in taxonomic composition and distribution from the base towards the top of the Nago shallowing-upward parasequences. Some general patterns can be recognized and interpreted according to data and ob-

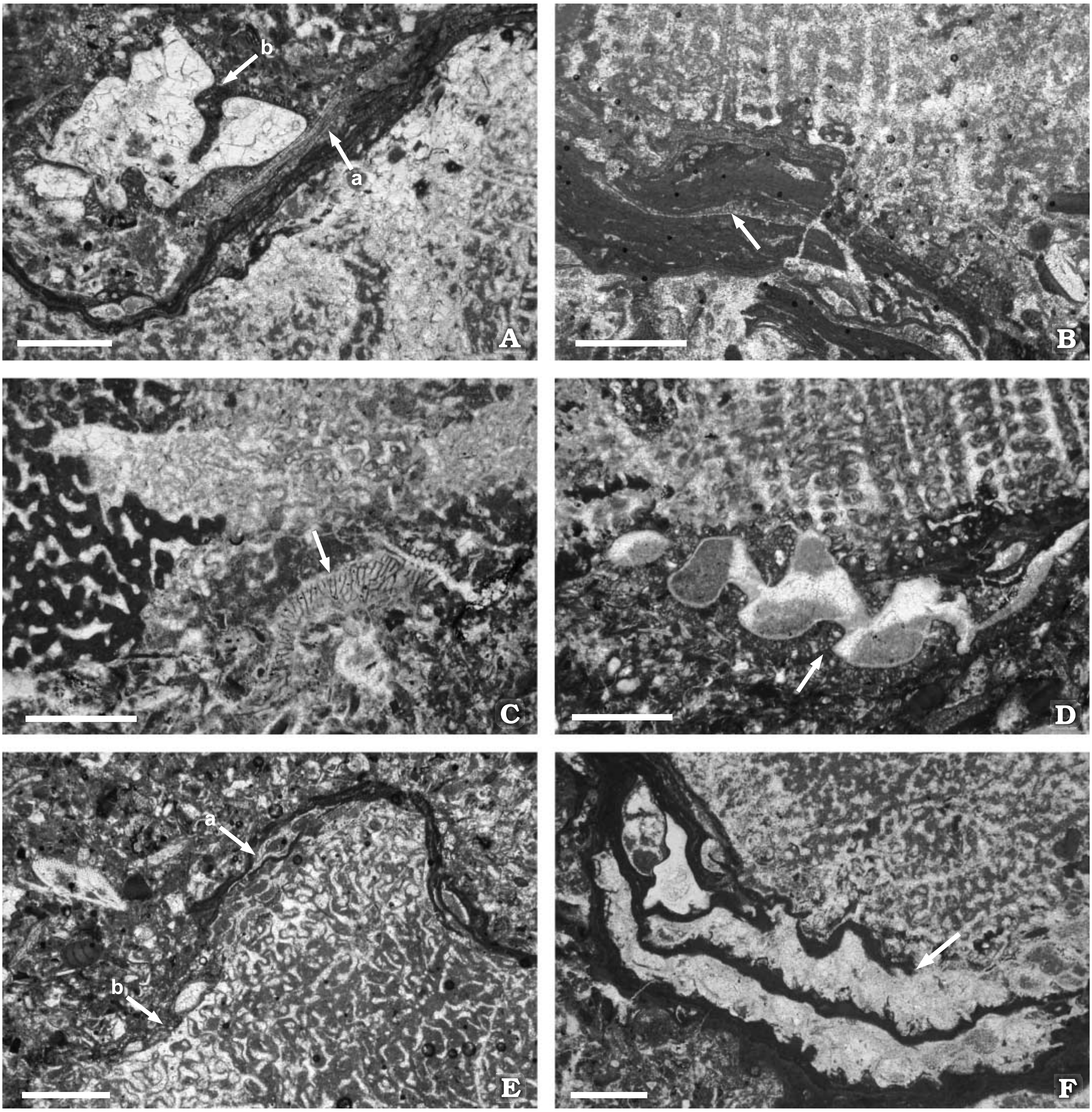

Fig. 7. Encrusting foraminiferans of Facies 2. **A**. IPUM 27827, foralgal crust with *Acervulina linearis* Hanzawa, 1947 (a) and a large *Haddonia*? sp. (b) on the upper surface of the coral *Actinacis rollei*. **B**. IPUM 27828, foralgal crust with *Acervulina linearis* Hanzawa, 1947 encrusting the lower surface of the coral *Actinacis rollei*. **C**. IPUM 27829, tangential section of *Fabiania cassis* (Oppenheim, 1896) encrusting the lower surface of the coral *Actinacis rollei*. **D**. IPUM 27830, *Haddonia heissigi* Hagn, 1968 encrusting the lower surface of the coral *Actinacis rollei*. **E**. IPUM 27831, thin foralgal crust with *Miniacina* sp. 1 (a) and a small *Haddonia heissigi* Hagn, 1968 (b) on the upper surface of the coral *Actinacis rollei*. **F**. IPUM 27828, well developed foralgal crusts with two specimens of *Planorbulina* aff. *uva* Scheibner, 1968 on the coral lower surface; note *P.* aff. *uva* overgrowing the algae (arrow). Scale bar 1 mm.

servations from present-day environments where, generally speaking, light intensity and water energy, together with competition for space and resources, are considered to be chief factors controlling distribution and morphological variation of encrusting foraminiferans (Martindale 1992; Perrin 1992; Elliott et al. 1996).

Several aspects characterize variations in the encrusting assemblages across the relative palaeobathymetric gradient

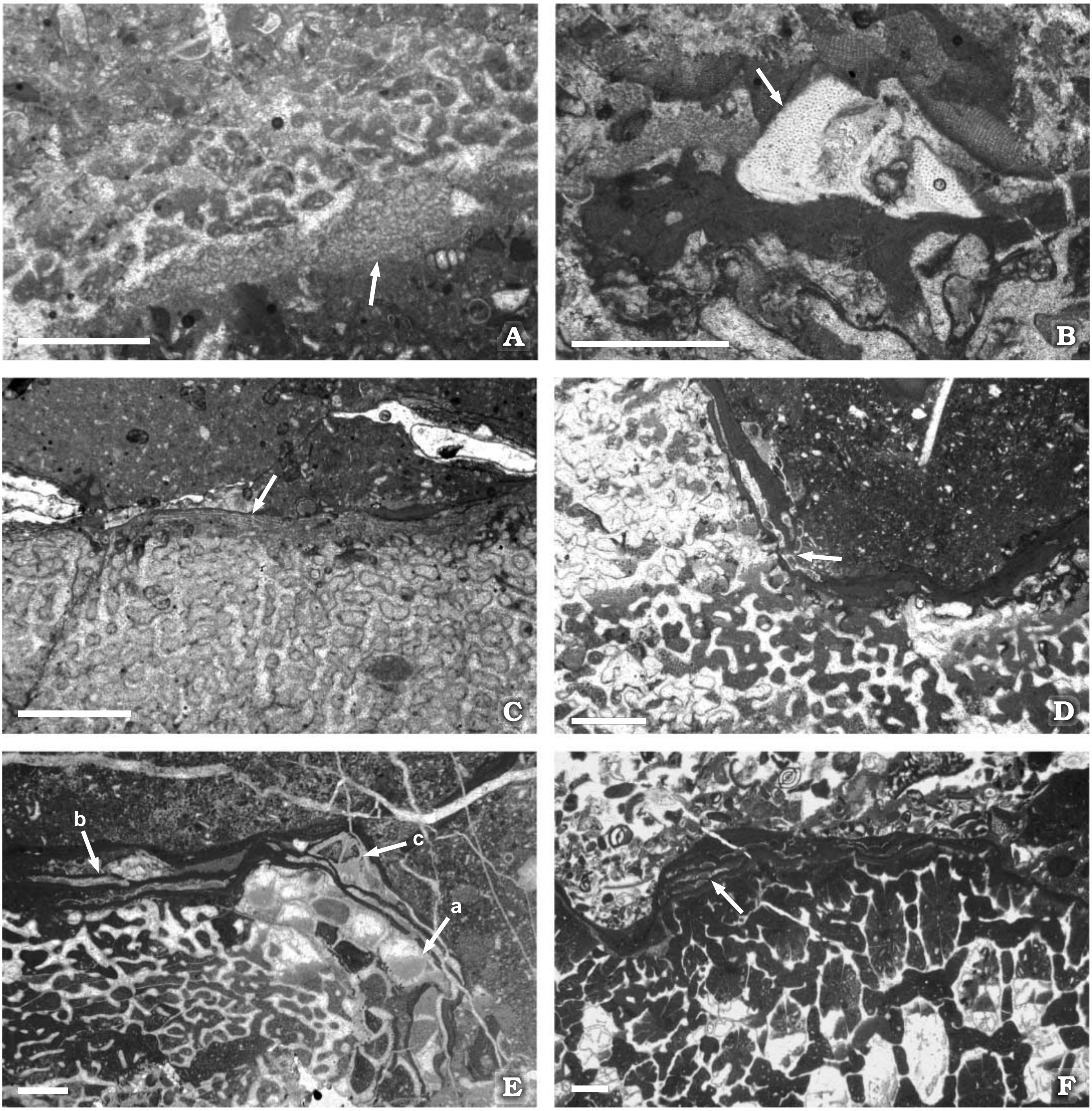

Fig. 8. Encrusting foraminiferans of Facies 3. **A**. IPUM 27832, *Solenomeris* sp. encrusting the lower surface of the coral *Actinacis rollei*. **B**. IPUM 27833, *Carpenteria* sp. encrusting the upper surface of the coral *Actinacis rollei*. **C**. IPUM 27834, *Acervulina linearis* Hanzawa, 1947 encrusting the upper surface of the coral *Actinacis rollei*. **D**. IPUM 27835, foralgal crust with *Miniacina* sp. 1 on the upper surface of the coral *Actinacis rollei*. **E**. IPUM 27836, foralgal crust with *Planorbulina* aff. *uva* Scheibner, 1968 (a), *Miniacina* aff. *multiformis* Scheibner, 1968 (b), and Victoriellidae (c) on the upper surface of the coral *Acropora*. **F**. IPUM 27837, foralgal crust with *Miniacina* aff. *multiformis* Scheibner, 1968 on the upper surface of the coral *Astreopora tecta*. Scale bar 1 mm.

represented by the succession of the three previously described facies.

First, abundance and species richness of encrusting foraminiferans reach their maximum in Facies 2. This fits very well the data from modern reefs (Dullo et al. 1990; Martindale 1992), where diversity and abundance are maximal at mid-depth in semi-cryptic (gloomy) environments. Species richness decreases in both shallower and deeper waters, whereas abundance only decreases with water depth.

In all three facies, isolated encrusting foraminiferans observed on coral upper surfaces are relatively few (Fig. 6). At all depths, they are in fact restricted to cryptic or semi-cryptic microhabitats (coral lower surfaces or sheltered upper surfaces), being unable to compete with the crustose coralline algae on exposed surfaces where they mainly occur as a subordinate component of crusts.

Encrusting foraminiferans within crusts formed on coral upper surfaces are more abundant in Facies 1 where, most probably, low light levels reduced their competition with coralline algae. However, the mid-depth reef slope with scattered large platy corals (Facies 2) seems to represent the most favourable environment for the development of these types of crusts, that also grew abundantly underneath coral plates (Dullo et al. 1990).

Present-day data, especially those concerning the ecology of two of the most common encrusting foraminiferans, *Miniacina* and *Homotrema*, suggest that test morphology is mainly controlled by water energy, with globose morphotypes dominating low-energy, more protected habitats and flat-encrusting tests typifying exposed substrates under high-energy conditions (Brasier 1975; Ghose 1977; Reiss and Hottinger 1984; Fagerstrom 1987; Martindale 1992; Elliott et al. 1996). Analogously, the flat *versus* globose morphotype ratio that has been calculated for the Nago specimens shows an increase from 2:1 in Facies 1 to 5:1 in Facies 3 (Fig. 9), indicating a positive correlation with a relative increase in water energy across the shallowing upward parasequence (Bosellini 1998).

Within each facies it can also be observed that flat morphotypes seem to be more successful on coral lower surfaces where relatively low light levels reduce competition with coralline algae (more space availability) allowing foraminiferans to spread laterally, sometimes overgrowing coralline algae (Fig. 7F). On the contrary, globose morphotypes seem to prefer coral upper surfaces where, with increasing lateral spatial competition with algae, they must expand their tests vertically to remain over algal crusts as long as possible. This growth strategy and morphological plasticity is particularly remarkable in *Solenomeris* (Facies 3), an "opportunistic" acervulinid foraminifer that formed monospecific reefs during Eocene time within the Tethyan palaeobiogeographic province (Perrin 1987; Plaziat and Perrin 1992).

The encrusting assemblage of Facies 3, partly similar to that of Facies 1, provides some interesting clues to the palaeoecological interpretation of this facies. Rather unexpectedly, foraminiferans encrusting coral upper surfaces are quite abundant and diversified.

Usually, light and turbulence increase from deep to shallow water, but this is not always the case with cryptic habitats as cavities and overhangs within dense coral fabrics in shallow water may be characterized by reduced levels of turbulence and illumination. Therefore, these kinds of microenvironments in shallow water provide sheltered habitats that can be colonized by encrusters normally found in deeper water (Martindale 1992). Within the Nago section, the species *Miniacina* aff. *multiformis*, typical of Facies 1, is quite common in Facies 3 and absent or rare in the more diversified Facies 2.

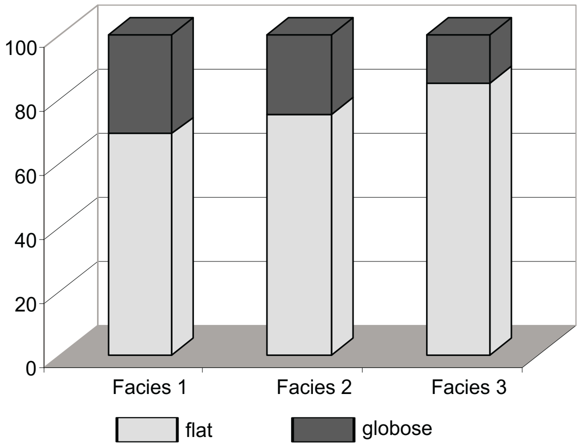

Fig. 9. Diagram showing the percentages of flat *versus* globose morphotypes of encrusting foraminiferans within Facies 1, Facies 2, and Facies 3.

Within this context, the dense coral growth fabric that locally characterized the shallowest part of the Nago reef front (Facies 3) and interpreted as being controlled by a relatively high hydrodynamic energy (Bosellini 1998), represented a shallow water shaded and protected habitat for encrusting foraminiferans. These data suggest that the type of growth fabric and coral cover can be considered another important factor controlling both composition and distribution of encrusting foraminiferans within the Nago sequence and, most probably, within reef settings in general.

The taxonomic composition of Eocene encrusting foraminiferans from Nago does not have a strictly equivalent modern counterpart for a valuable comparison and also studies about distribution of encrusting foraminiferans within recent and fossil reefs are few. However, some information can be gathered especially for those most abundant and extant genera such as *Acervulina*, *Miniacina, Haddonia,* and *Carpenteria.*

According to the present-day data on the ecology of Homotrematidae (*Miniacina* and *Homotrema*), these foraminiferans seem to prefer cryptic microenvironments, often on the underside of dead corals (Vasseur 1974; Brasier 1975; Ghose 1977; Fagerstrom 1987; Martindale 1992), although *Homotrema rubra* from Bermuda was observed on exposed reef surfaces too (Elliott et al. 1996) and *Miniacina* is an important component of the polygenic-micritic crusts that strongly bound *Porites* coral branches of the Late Miocene Mediterranean reefs (Bosellini et al. 2002).

A modern equivalent of *Acervulina linearis* could be *A. inhaerens* (or *Gypsina plana* according to Hottinger et al. 1993). This species is very common in the shallow waters of the Gulf of Aqaba and has an abrupt depth limit at 130 m, probably due to the disappearance of its food, benthic diatoms, near the limit of the euphotic zone. It grows (at least until 60 m of depth) on light-exposed surfaces but at very shallow depths it could be cryptic (Reiss and Hottinger 1984). *A. inhaerens* also occurs from 5 to 50 m in the Safaga Bay (Egypt) and is dominant below 40 m (Rasser and Piller 1997).

According to Perrin (1992), acervulinids generally dominate where light conditions reduce competition with coralline algae and their constructional role is enhanced in environments where ecologic conditions lead to the reduction of competition for substrate encrustation.

Concerning the genus *Haddonia*, the modern *H. torresiensis* from reef sites of Somali Coast and Java is described by Matteucci (1996) as a cryptic species common in shaded areas (underside of foliated coral colonies, basal cavities of crevices) or in the subdued light of intertidal environments. Data about the Eocene *H. heissigi* (Darga 1990; Matteucci 1996; Rasser 2000), together with results from the present study, show that the autoecology of this fossil species is very similar to that of *H. torresiensis*.

As regards modern encrusting species of the genus *Carpenteria*, characteristic of the shallower Facies 3 in Nago, they seem to prefer cryptic habitats in shallow environments (0 to 30 m depth) as observed in Tuléar (Madagascar) (Vasseur 1974), in Bermuda (Jones and Hunter 1991), in Barbados reefs (Martindale 1992), and in the Chagos Islands (Murray 1994).

Conclusions

Coral-encrusting foraminiferan associations and their variations along a palaeobathymetric gradient represented by the different facies that characterize the shallowing upward parasequences of the Nago Limestone (Upper Eocene, Trentino, northern Italy) have been investigated.

This study, besides providing new data to the generally poor knowledge of encrusting foraminiferans within fossil reef settings, has led to the following conclusions:

- From a relatively deep reef slope (Facies 1) up to the shallow shelf-edge (Facies 3), corals have been recognized to be encrusted by different foraminiferan assemblages that change in composition and distribution.
- Three main assemblages have been recognized and named according to the dominant and characteristic taxa: 1) *Miniacina* aff. *multiformis* assemblage (Facies 1); 2) *Acervulina–Fabiania–Haddonia* assemblage (Facies 2); and 3) *Solenomeris–Carpenteria* assemblage (Facies 3).
- Significant variations mainly concern the following features: taxonomic composition, relative abundance and diversity, encrusted coral surface, growth morphology and association with encrusting coralline algae.
- The succession of encrusting foraminiferan assemblages is interpreted to be controlled mainly by light, competition with coralline algae, hydrodynamic energy and coral growth fabric.
- Foraminiferans encrusting corals directly (not associated with algal crusts) mostly occur in cryptic habitats and especially on coral lower surfaces, whereas on exposed surfaces they generally contribute to form crusts together with coralline algae. These foralgal crusts preferentially develop along the mid-depth reef slope (Facies 2), on both upper and lower surfaces of the platy corals.
- Test morphology, and especially the flat *versus* globose morphotypes ratio, positively correlates with increasing water energy across the shallowing upward sequence. However, within this general trend, their preferential encrusted surface is mainly controlled by light and consequent competition with coralline algae. Flat specimens mostly encrust coral lower surfaces where low light levels generally reduce competition for space with coralline algae. In contrast, globose morphotypes are successful on coral upper surfaces, where lateral spatial competition with algae is higher.
- The dense coral growth fabric that characterizes the shallower portion of the Nago reef front, provided cryptic habitats for the development of an encrusting foraminiferan assemblage partly similar to the one recognized within the relatively deep and poorly illuminated reef slope.

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Appendix

Taxonomic list of encrusting foraminiferans in the Nago section.

- Order Foraminiferida Eichwald, 1830
  - Suborder Textulariina Delage and Hérouard, 1896
    - Superfamily Lituolacea de Blainville, 1827
      - Family Placopsilinidae Rhumbler, 1913
        - Subfamily Placopsilininae Rhumbler, 1913
          - Genus *Placopsilina* d'Orbigny, 1850
            - *Placopsilina*? sp.
            - *Placopsilina* sp. 1
    - Superfamily Coscinophragmatacea Thalmann, 1951
      - Family Haddoniidae Saidova, 1981
          - Genus *Haddonia* Chapman, 1898
            - *Haddonia*? sp.
            - *Haddonia heissigi* Hagn, 1968
      - Family Coscinophragmatidae Thalmann, 1951
          - Genus *Bdelloidina* Carter, 1877a
            - *Bdelloidina* sp. 1
  - Suborder Rotaliina Delage and Hérouard, 1896
    - Superfamily Planorbulinacea Schwager, 1877
      - Family Planorbulinidae Schwager, 1877
        - Subfamily Planorbulininae Schwager, 1877
          - Genus *Planorbulina* d'Orbigny, 1826
            - *Planorbulina bronnimanni* Bignot and Decrouez, 1982
            - *Planorbulina* aff. *uva* Scheibner, 1968
            - *Planorbulina* sp. 1
      - Family Cymbaloporidae Cushman, 1927
        - Subfamily Fabianiinae Deloffre and Hamaoui, 1973
          - Genus *Eofabiania* Küpper, 1955
            - *Eofabiania* sp.
          - Genus *Fabiania* Silvestri, 1924
            - *Fabiania cassis* (Oppenheim, 1896)
      - Family Victoriellidae Chapman and Crespin, 1930
      - Victoriellidae indet.
        - Subfamily Carpenteriinae Saidova, 1981
          - Genus *Carpenteria* Gray, 1858
            - *Carpenteria* sp.
    - Superfamily Acervulinacea Schultze, 1854
      - Family Acervulinidae Schultze, 1854
          - Genus *Acervulina* Schultze, 1854
            - *Acervulina linearis* Hanzawa, 1947
          - Genus *Gypsina* Carter, 1877b
            - *Gypsina globula* (Reuss, 1848)
            - *Gypsina mastelensis* Bursch, 1947
            - *Gypsina moussaviani* Brugnatti and Ungaro, 1987
          - Genus *Solenomeris* Douvillé, 1924
            - *Solenomeris* sp.
      - Family Homotrematidae Cushman, 1927
          - Genus *Miniacina* Galloway, 1933
            - *Miniacina multicamerata* (Scheibner, 1968)
            - *Miniacina* aff. *multiformis* Scheibner, 1968
            - *Miniacina* sp. 1