

# Larger foraminifera as a substratum for encrusting bryozoans (Late Oligocene, Tethyan Seaway, Iran)

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Received: 15 July 2008 / Accepted: 4 November 2008  
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**Abstract** Considering the diversity and abundance of larger foraminifera examined from a wide range of Late Oligocene to Early Miocene palaeoenvironments in the Tethyan Seaway, encrusting bryozoans make extremely little use of their tests as substratum. Significant encrustations by bryozoans were exclusively found on large ( $\varnothing$  c. 6 cm), undulating tests of *Lepidocyclina* spp., on which, however, a remarkable 34 taxa of encrusting bryozoans were recorded. This shallow-water fauna of Chattian age was analyzed in respect of the bryozoan taxa present, colony growth type, and mode of budding, colony size, as well as onset of reproduction. Taxic and morphological similarities between the fossil assemblage and modern faunas encrusting mobile substrata indicate a long history of bryozoans as part of the interstitial habitat, while the tests of certain larger foraminifera may have played a significant role in the evolution of shallow-water bryozoans by providing substrata for encrusting species in otherwise unfavorable environments.

**Keywords** Bryozoa · Interstitial · Larger foraminifera · Palaeoecology · Tethys

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## Introduction

In tropical shallow-water environments, encrusting bryozoans usually occupy cryptic habitats owing to their inferiority to other clonal and/or phototrophic organisms (such as scleractinian corals, ascidians, algae, and sponges) in competition for space (e.g., Jackson and Winston 1982; Jackson 1984; McKinney and Jackson 1989). Displacement of relatively slow-growing bryozoans to undersurfaces of corals or to cryptic environments is especially prevalent on large stable substrata, on which community composition is generally controlled by post-recruitment interactions among established organisms (Winston and Jackson 1984; McKinney and Jackson 1989; p. 110, 145). In contrast, the composition of communities on ephemeral or unstable substrata, which can easily be moved about, is primarily determined by recruitment rates as well as by active habitat selection of larvae and directional growth of the colony (e.g., Buss 1979; Jackson 1979; Bishop 1989). Accordingly, in coral reefs, bryozoans are more diverse and abundant in cryptic habitats and on fragments of dead corals, molluscs, and echinoids (e.g., Cuffey 1973; Jackson and Winston 1982; Choi and Ginsburg 1983; Kobluk et al. 1988; Meesters et al. 1991), and may even form a significant component of the subtidal meiofauna, encrusting single sand-sized grains (Håkansson and Winston 1985; Winston and Håkansson 1986; Winston and Migotto 2005).

One common constituent of unstable, bioclastic deposits in the tropical to subtropical photic zone, and therefore a potential substratum for encrusting bryozoans, are tests of larger foraminifera. These symbiont-bearing protists range in size from less than a centimeter to some 15 cm in diameter and produce flat, lenticular or undulating tests (e.g., Drooger 1993; Hallock 1999; Beavington-Penney and Racey 2004). Larger foraminifera may occur in rock-forming

abundance, especially during the Paleogene, such as in the Eocene nummulitic limestones that today crop out around the Mediterranean Sea (e.g., Aigner 1983; Beavington-Penney et al. 2005). Their large size and occasionally irregular surface topography may provide a range of microhabitats as well as relatively large subsurface cavities in the form of interparticle pores in foraminiferal deposits. The model for unilaminar growth patterns in cheilostome bryozoans (Bishop 1989) implies that colonies on spatially predictable and restricted, unstable substrata, such as larger foraminiferal tests, should display patch and spot colony forms. In general, these are characterized by relatively small colonies that grow by intrazoidal or zooidal budding (cf. Lidgard 1985), reach sexual maturity during early colony development, and occasionally show determinate growth (Bishop 1989).

Records of modern bryozoans encrusting foraminiferal tests are sparse: Cook (1968a, 1985) reported a total of 24 bryozoan species off tropical West Africa encrusting *Jullienella foetida* Schlumberger, a fan-shaped agglutinated foraminifer accreting sand grains, as well as the hyaline perforated *Cycloclypeus carpenteri* Brady, in depths of 20–65 m and 50–70 m, respectively. In addition, Yordanova and Hohenegger (2002) mentioned the presence of bryozoans on the hyaline perforated *Baculogypsinoidea spinosus* Yabe and „Hanzawa, *Operculina ammonoides* (Gronovius), and also *C. carpenteri* off southern Japan.

Records of fossil bryozoans using larger foraminifers as substratum are similarly few in number. Cheetham (1963: p. 32, table 13) recorded a Late Eocene association between several bryozoan species and “larger foraminifera” of the eastern Gulf of Mexico region but did not go into further detail. Furon and Balavoine (1959), who analyzed material from the Early Miocene of the same region as the present study (see below), reported several bryozoan species to encrust lepidocyclinid tests.

The aim of this paper is therefore to assess the use of tests of larger foraminifera as a substratum by encrusting bryozoans, with special emphasis on the palaeoenvironment as well as colony growth and reproduction strategies of both the foraminifers and bryozoans. The studied material is from the Late Oligocene of central Iran, which was then situated at the northern margin of the Tethyan Seaway that connected the proto-Indo-Pacific with the Western Tethys region.

### Geological setting

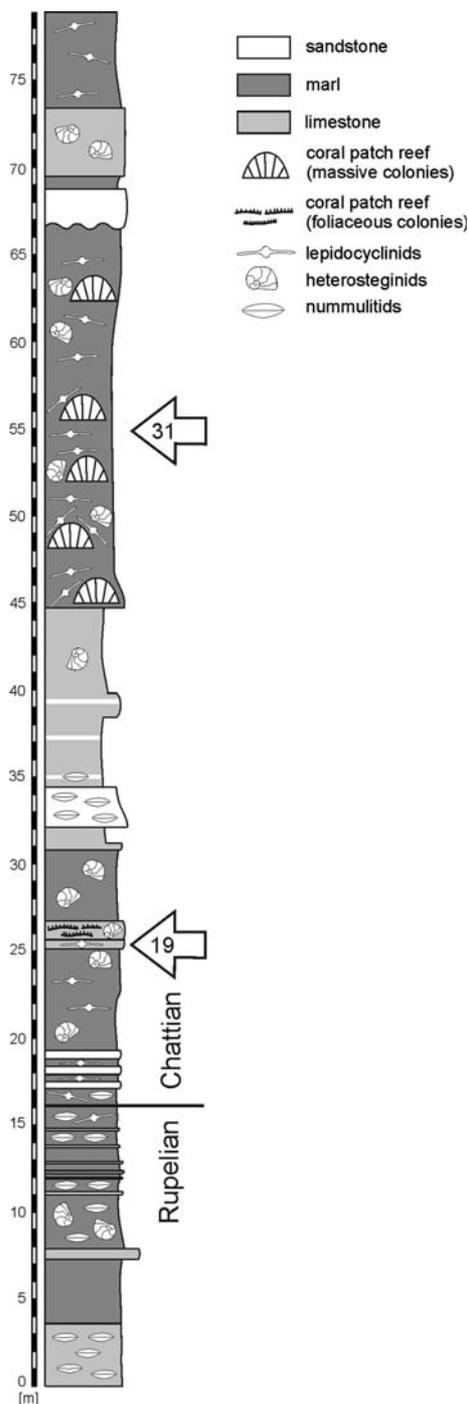
During the Late Oligocene, the narrowing Tethyan Seaway formed the connection between the Eastern Tethys (the proto-Indian Ocean) and the Western Tethys region (the proto-Mediterranean Sea). Subduction of the African–Arabian

Plate underneath the Eurasian plates led to the formation of a volcanic arc and compartmentalization of the region, creating the Esfahan–Sirjan fore-arc and the Qom back-arc basins at the northern margin of the Tethyan Seaway (e.g., Rögl 1998; Harzhauser et al. 2007; Reuter et al. 2008). Before final closure of the seaway during the latest Early Miocene, thick limestone and marl successions (the Qom Formation) were formed in both basins, which today crop out east of the Zagros thrust fault in central Iran (Fig. 1). Two stratigraphical sections in each basin were studied within a larger Austrian–German research project: the sections Zefreh and Abadeh in the Esfahan–Sirjan Basin, and the sections Qom and Chalheghareh in the Qom Basin [see Reuter et al. (2008) for detailed information].

Although thin sections and isolated foraminifera from all sections were screened for encrusting bryozoans, the analytical part of this work concentrates on the Abadeh section in the Esfahan–Sirjan fore-arc basin only (Figs. 1, 2). This section comprises Middle to Upper Oligocene sediments that were deposited on a gently inclined ramp. Facies analyses based on field observations, thin sections, and palaeontological studies indicate that palaeoenvironments ranged from outer ramp to intertidal settings. The limestones and marls were formed by different coral assemblages, coralline algae, diverse and abundant larger foraminiferal faunas, and planktic organisms, respectively (Reuter et al. 2008).



**Fig. 1** Location of the studied section Abadeh, central Iran. The extent of the Esfahan–Sirjan fore-arc (ESB) and Qom back-arc basins (QB) are marked by light grey shading, whereas the volcanic arc (VA) is represented by a dark grey area. The serrated line marks the Zagros thrust fault (for more detailed information see Reuter et al. 2008)



**Fig. 2** Lower part of the measured section Abadeh (mid-Oligocene), containing diverse and abundant assemblages of larger foraminifera. Whereas foraminifera from all beds were screened for encrusting bryozoans, only the lepidocyclinid assemblages of beds 19 and 31 (arrows), comprising thick, large and undulose foraminiferal tests, yielded encrusting bryozoans. For chronostratigraphic information, description of lithology, identified depositional sequences, and palaeo-environmental interpretation see Reuter et al. (2008)

Larger benthic foraminifera are prevalent especially in the lower and middle part of the c. 160-m-thick section, ranging in age from latest Early Oligocene to middle Late

Oligocene, and are mainly represented by nummulitids and lepidocyclinids (Schuster and Wielandt 1999). Bryozoans occasionally play a significant role in carbonate production but only in the deeper environments where they may co-occur with larger foraminifera and in which erect growth forms then dominate. In contrast, encrusting bryozoans are distinctly less conspicuous and their contribution to carbonate production is insignificant apart from locally abundant growth of celleporiform colonies (Reuter et al. 2008).

## Material and methods

In contrast to the cemented, pure limestone, which was examined in thin sections only, the isolated larger foraminifera used in this study come from marly sediments that could be disaggregated and washed, and in which the surfaces of bioclasts remained free of excessive cement. These marls preferentially occur in the lower part of the Abadeh section (Fig. 2) and contain mass occurrences of *Nummulites sublaevigatus* at the base and more diverse assemblages of lepidocyclinids and nummulitids (e.g., *Operculina*, *Heterostegina*) further upsection (see Schuster and Wielandt 1999; Reuter et al. 2008). Several thousand (fragments of) isolated larger foraminifera were screened for encrusting bryozoans. Test sizes range from millimeter-sized *Amphistegina* sp., *Archaias* spp., *Borelis* spp., *Heterostegina* spp., *Miogypsinoides* spp., *Operculina* spp., and *Peneroplis* spp., to centimeter-sized *Nummulites sublaevigatus*, to large *Lepidocyclina* (*Eulepidina*) aff. *dilatata concentrica* of >6 cm in diameter. The bulk of the foraminiferal tests comprise highly diverse *Lepidocyclina*, *Nephrolepidina* and *Eulepidina* assemblages. Whereas the small foraminiferal tests were usually preserved whole, the large lepidocyclinids are generally fragmented due to compaction. Moreover, pressure dissolution at grain contacts occasionally affects surface structures (cf. Hageman et al. 2004). The fragmentary preservation of most lepidocyclinid tests thus inhibits a rigorous analysis of bryozoan settlement sites, growth and reproduction patterns in relation to the available surface. A direct comparison with previous results of similar studies on bryozoans encrusting disarticulated but entirely preserved bivalve shells, which provided surfaces that could be normalized (Bishop 1988, 1994; Ward and Thorpe 1989; Reguant and Mayoral 1994; McKinney 2000), is therefore not feasible and measurements must remain semi-quantitative.

Foraminifera with encrusting bryozoans were treated with the tenside Rewoquat in order to remove clay particles, and were subsequently cleaned in an ultrasonic bath. The dried specimens were then taxonomically determined with the aid of a binocular microscope. However, although showing little signs of post-mortem physical abrasion, the

preservation of bryozoan zoecia allows for assignment to generic level at best because of neomorphism of the original skeleton and filling of the apertures with particles that resisted removal. The unilaminar encrusting growth habit was further subdivided and characterized as runner, ribbon, spot, patch and sheet (*sensu* Bishop, 1989), reflecting different ‘strategies’ in the competition for and exploration of space (e.g., Buss 1979; Jackson 1979; Taylor 1999; Okamura et al. 2001). Although Bishop’s (1989) classificatory model was developed for unilaminar encrusting cheilostome Bryozoa, the terms for colony growth forms are here also employed for cyclostomes (see also McKinney and Taylor 1997).

The number of colonies per taxon was recorded whereas no distinction was made between entire or partial preservation of the zoaria. As a measure of colony size, the number of zooids in each colony was determined. However, in case of partial preservation of the colony, which commonly occurred due to fragmented preservation of foraminiferal tests, this value may greatly underestimate the true colony size. In colonies of cheilostome bryozoans where the ancestrula was present, representing the position of larval settlement and metamorphosis, the number of zooids was estimated that were budded before formation of the first ovicell, indicating embryonic brooding and hence female sexual maturation of the colony.

## Results

### Tests of larger foraminifera as a substratum

Examination of the isolated larger foraminiferal tests from the mid-Oligocene to Lower Miocene sections Abadeh, Zefreh, Chalheghareh, and Qom (see Reuter et al. 2008) showed that these potential substrata are rarely used by encrusting bryozoans. Although the examined foraminifera are from a wide range of environments and comprise a wealth of different morphotypes, only very few beds composed of large lepidocyclinids yielded tests with an appreciable number of bryozoan colonies and taxa present. Palaeoenvironmental reconstructions were achieved by analyzing both foraminiferal assemblages and the associated biota (Reuter et al. 2008). Palaeoenvironments comprise very shallow habitats, such as patch reefs and reef rubble (with *Amphistegina*, *Borelis*) as well as seagrass meadows (with *Archaias*, *Peneroplis*), and near-shore environments influenced by siliciclastics (with *Nummulites*). Shallow turbid waters as well as deeper environments of the mid- to outer-ramp are especially characterized by diverse lepidocyclinid assemblages, the tests of which may reach several centimeters in diameter [for palaeoenvironmental reconstructions and references see Schuster and Wielandt (1999) and Reuter et al. (2008)].

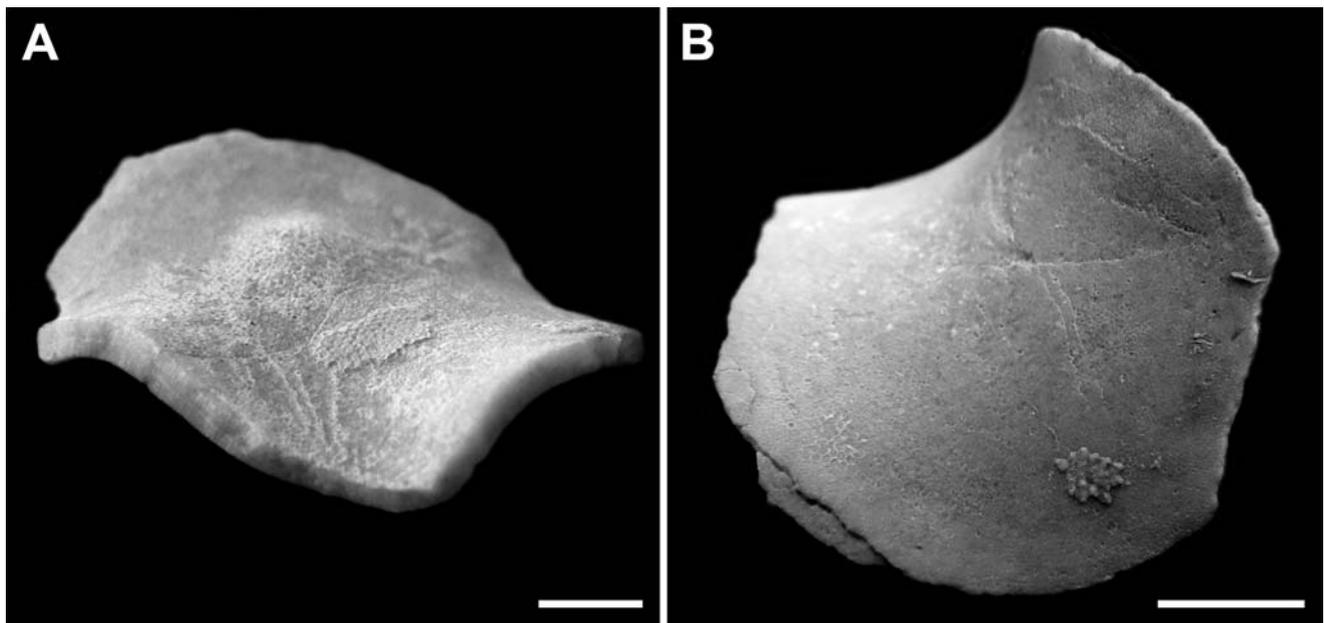
The shapes of foraminiferal tests range from spherical or ellipsoidal (*Borelis*), to lenticular (*Amphistegina*, *Miogypsinoides*, *Nummulites*, some *Lepidocyclina*), to flat (*Archaias*, *Heterostegina*, *Operculina*, *Peneroplis*, some *Lepidocyclina*), to undulose (some *Lepidocyclina*). Encrusting bryozoans were exclusively found on tests of *Lepidocyclina* spp., which formed undulating tests of variable thickness and size (Fig. 3). No other foraminifera yielded encrusting colonies. Thin-section analysis corroborated this observation on isolated foraminifera.

Furthermore, a sufficiently diverse, abundant and well-preserved encrusting bryozoan fauna on *Lepidocyclina* tests adequate for an analysis was provided by bed 31 (early Chattian) of section Abadeh only (Fig. 2). These lepidocyclinids occur in marls that form the base of a shallowing-upward subcycle, which terminates with small coral patch reefs constructed by *Porites* and faviids (Schuster and Wielandt 1999). Some five, mostly indeterminate, lepidocyclinid species are present, whereas most bryozoan colonies encrust the irregularly undulating, large and thick tests of *L. (E.) aff. dilatata concentrica* Silvestri (Fig. 3a). The analysis of bryozoan growth and reproduction strategies presented below is therefore exclusively based upon specimens from this bed. Saddle-shaped tests of another, unidentified lepidocyclinid from bed 19 (Figs. 2, 3b), interpreted to have formed in deeper waters on the mid-shelf, were encrusted by too few bryozoan colonies to be further considered here.

Of a total of 1,640 lepidocyclinid fragments screened from bed 31, ranging in diameter between c. 2 mm to 6 cm, 167 (≈10%) were encrusted by bryozoans. Test fragments towards the upper end of the grain-size spectrum yielded bryozoan colonies more frequently, which is related to the scarce spatial cover of the tests by bryozoans (see below). The foraminiferal tests and test fragments are well-preserved and show no taphonomic signatures apart from pressure-related damage owing to compaction of the sediment.

### The encrusting bryozoan fauna

While 34 bryozoan taxa were identified encrusting lepidocyclinid tests (Table 1) this number needs to be regarded as conservative because of relatively poor preservation of the zoecia (Fig. 4). Neomorphism of the bryozoan skeleton and filling of apertures by clastic material, both inhibiting examination of taxonomically important morphological details, precluded a more precise determination at species level or unequivocal assignment to a particular taxon in every case. For example, it is likely that *Puellina* sp. 2 comprises several species as specimens were grouped with this taxon when characteristics of other *Puellina* spp. could not be observed. On the other hand, the bryozoan zooidal skeletons and colonies rarely show signs of pre-burial damage,



**Fig. 3** Encrusted tests of lepidocyclinids from the Abadeh section, mid-Oligocene. **a** An undulose test of *Lepidocyclina (E.) aff. dilatata concentrica* Silvestri with a patch colony of *Onychocella* sp. (bed 31);

scale bar 4 mm. **b** An unidentified, saddle-shaped lepidocyclinid with a spot colony of *Escharina* sp. (bed 19); scale bar 4 mm

indicating little or no reworking (Fig. 4). Several additional taxa are present on lepidocyclinid tests from assemblages of the remaining sections, which are, however, not considered here due to their infrequent occurrence. Other groups of organisms encrusting lepidocyclinids were seldom observed but included serpulids as well as other benthic foraminifera (?*Cibicidoides*, *Placopsilina*).

The bryozoan fauna is represented by a wide range of higher taxa, with cheilostomes being predominant as only six cyclostome species are present (Table 1). Within the Cheilostomata, species belonging to genera of the family Cribrilinidae prevail in numbers (*Cribrilina* sp., *Distansescharella* sp., *Puellina* sp. 1–4). Species of the Escharinidae form the second most abundant group [*Bryopesanser* sp., *Escharina* sp., *Herentia* sp., *Therenia* sp. (Fig. 4e)]. Concerning colony number and colony size, the anascan *Micropora* sp. (Fig. 4b) stands out with many colonies comprising over 100, and some exceeding 200 zooids. Although more specimens were recorded for *Puellina* sp. 2, this number may be exaggerated (see above). Nevertheless, most species are rare while only four species show high abundances that make up for 50% of the total assemblage (including *Puellina* sp. 2). Bryozoan colonies of a few species with erect growth were present in the matrix but encrusting bases on the foraminiferal tests were never observed.

#### Bryozoan growth and reproductive patterns

A total of 311 colonies and colony fragments of encrusting bryozoans were recorded on 167 fragments of *Lepidocy-*

*clina* spp. (Table 1). Although up to 18 colonies were observed on a c. 5 cm<sup>2</sup> fragment of *L. (E.) aff. dilatata concentrica*, settling on both sides of the test, colony size was usually small and the occupied space therefore limited. As a consequence, overgrowth interactions are rarely observed and smaller foraminiferal test fragments are often devoid of encrusting bryozoans. Furthermore, while most of the larger test fragments are encrusted on both sides, smaller fragments usually exhibit colonies growing on one side only. The site of larval settlement and metamorphosis into an ancestrula was always observed to be at some distance from the prominent central nepionic apparatus of the lepidocyclinids. In addition, only large colonies of *Micropora* sp. were found to encrust the central region in a few instances.

Mode of colony growth in the cheilostomes present is predominantly of the intrazooidal type while only a few taxa, e.g., *Escharoides* sp. and *Smittoidea* sp., show zooidal or multizooidal budding, respectively (cf. Lidgard 1985). Most bryozoan taxa form colony types that are, in the terminology of Bishop (1989), classified as spots (18 ≈ 53%), whereas ten taxa form patches (30%), three runners (9%), two ribbons (6%), and one (3%) comprises mound-like celleporiform colonies. A patch is here arbitrarily distinguished from a spot colony if it consists of more than 100 zooids (see also Discussion). There were no species with colonies exclusively consisting of fewer than ten zooids. Colonies of three taxa comprised 20 or fewer zooids, whereas there were between 21 and 50 zooids in colonies of eight taxa, between 51 and 100 zooids in colonies of 13

**Table 1** Census data of encrusting bryozoan taxa present on lepidocyclinid tests (bed 31, section Abadeh) concerning their colony growth type, the number of colonies present, size of colonies, number

of colonies with ancestrulae and ovicells, and the number of zooids present before formation of the first ovicell in cheilostome species

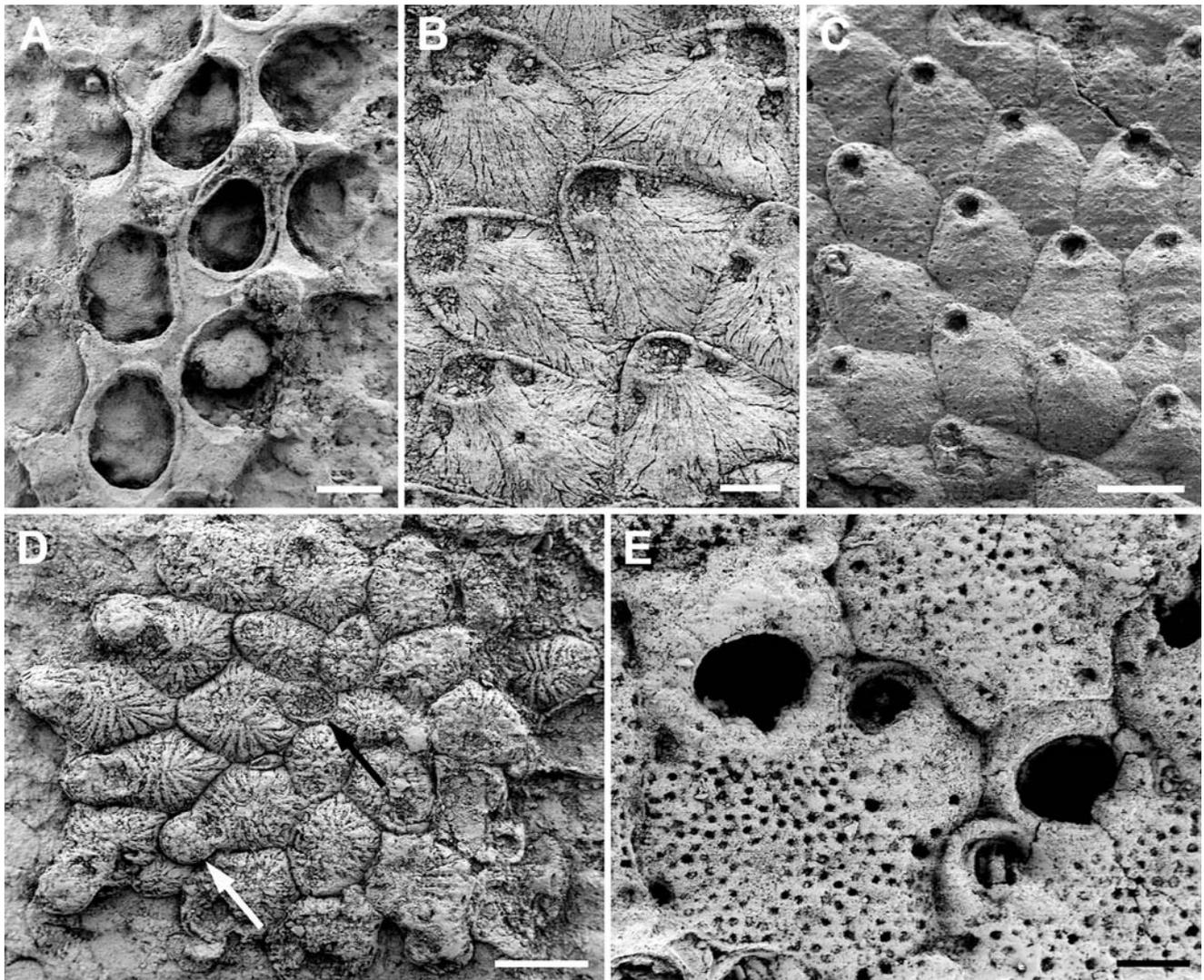
Taxon	ColGrF	Cols	%	Zooids per colony						CwAnc	CwOv	Ovicells formed after ... zooid					
				1-10	11-20	21-50	51-100	>100	>200			1-5	6-10	11-20	>21		
<i>Annectocyma</i> sp.1	Ribbon	5	1.6	2	3					4							
<i>Annectocyma</i> sp.2	Ribbon	1	0.3			1											
<i>Bryopesanser</i> sp.	Spot	3	1.0		1	2				3	1		1				
<i>Callopora</i> sp.	Spot	2	0.6			2				1	1	1					
Celleporidae indet.	Mound	4	1.3			1	2	1		1							
Cheilostomata indet.1	Patch	13	4.2	1	3	5	3	1		5							
Cheilostomata indet.2	Spot	7	2.3	2	3	1	1			4	1	1					
Cheilostomata indet.3	Spot	1	0.3		1												
Cheilostomata indet.4	Spot	1	0.3			1											
Cheilostomata indet.5	Spot	1	0.3				1										
Cheilostomata indet.6	Spot	1	0.3				1			1							
<i>Copidozoum</i> sp.	Spot	2	0.6		1	1				1	1				1		
<i>Cribrilina</i> sp.	Patch	21	6.8	3	5	8	4	1		13	4				1		3
Cyclostomata indet.	Runner	8	2.6		4	3	1			2							
<i>Diplosolen</i> sp.	Spot	7	2.3		1	4	2			6							
<i>Disporella</i> sp.	Spot	8	2.6		3	5				8							
<i>Distansescharella</i> sp.	Spot	4	1.3	1		2	1			3	1				1		
? <i>Escharella</i> sp.	Patch	5	1.6		1		2	2		1	1		1				
<i>Escharina</i> sp.	Spot	4	1.3	1	1	1	1			1	1				1		
<i>Escharoides</i> sp.	Patch	6	1.9		2	2		2		2	1		1				
<i>Herentia</i> sp.	Spot	3	1.0		1	2				2	1						1
<i>Hippothoa</i> sp.	Runner	1	0.3				1										
<i>Micropora</i> sp.	Patch	48	15.4	2	2	9	15	17	3	8	1				1		
<i>Monoporella</i> sp.	Spot	4	1.3			2	2			2							
<i>Onychocella</i> sp.	Patch	12	3.9			7	3	2		1							
<i>Puellina</i> sp.1	Spot	14	4.5	1	2	7	4			6	3				3		
<i>Puellina</i> sp.2	Patch	69	22.2	7	14	26	19	3		28	12		2		1		9
<i>Puellina</i> sp.3	Spot	5	1.6	2		2	1			5	5	2	3				
<i>Puellina</i> sp.4	Patch	3	1.0			1	1	1									
<i>Pyripora</i> sp.	Runner	1	0.3		1												
<i>Smittoidea</i> sp.	Patch	1	0.3			1											
<i>Therenia</i> sp.	Spot	10	3.2		3	5	2			4	1						1
<i>Trypostega</i> sp.	Patch	23	7.4		1	9	12	1		2	1						1
<i>Tubulipora</i> sp.	Spot	12	3.9	1	4	6	1			12							
Sum		311	99.7														

ColGrT, Colony growth type; Col#, Number of colonies; CwAnc, Number of colonies with an ancestrula; CwOv, Number of colonies of cheilostomes with an ancestrula in which ovicells are present

taxa, over 100 zooids in colonies of nine taxa, and over 200 zooids only in some colonies of *Micropora* sp. (Table 1). However, these numbers have to be regarded as minimum values due to fragmentary preservation, especially of the larger and runner-type colonies.

Accordingly, the ancestrula is more frequently present in spot-, ribbon- and smaller patch-colony types, and only a

fraction of those colonies of cheilostome bryozoan taxa in which the ancestrula was preserved also yielded ovicells. A single species (*Puellina* sp. 3) showed an unambiguous pattern, producing ovicells before formation of the tenth zooid in all colonies. Due to strong neomorphism, the identification of gonozooids in cyclostome colonies was rendered difficult and maturation in these taxa is not further considered here.



**Fig. 4** Selected bryozoans encrusting lepidodyclinid tests (Abadeh section, bed 31). **a** *Callopora* sp.; scale bar 200  $\mu$ m. **b** *Micropora* sp., forming the largest patch colonies (bed 31); scale bar 100  $\mu$ m. **c** *Try-*

*postega* sp.; scale bar 200  $\mu$ m. **d** A spot colony of *Puellina* sp. 3; note the central ancestrula (black arrow) and early onset of ovicell formation (white arrow). Scale bar 200  $\mu$ m. **e** *Therenia* sp.; scale bar 100  $\mu$ m

## Discussion

### Tests of larger foraminifera as a substratum

Although bryozoans are known to encrust single sand-sized grains in interstitial, shallow-water, sedimentary environments (Håkansson and Winston 1985; Winston and Håkansson 1986), the tests of fossil larger foraminifera analyzed in this study were rarely used as substratum. Colonies of encrusting bryozoans were almost exclusively found on larger tests of *Lepidocyclus* spp., which was also noted as a substratum by Furon and Balavoine (1959), who studied an Aquitanian bryozoan fauna from the Qom Basin. Furthermore, although lepidodyclinid tests occur throughout the studied sections, only a single bed in the Abadeh section (see Reuter et al.

2008) yielded a substantial number of encrusting bryozoan colonies.

Taxa with smaller tests (*Amphistegina*, *Archaias*, *Borelis*, *Heterostegina*, *Miogyopsinoides*, *Operculina*, *Peneroplis*, *Nummulites*) were not colonized by bryozoans, corroborating previous negative results from studies of other Neogene faunas. For instance, Braga and Bahr (2003), Bassi (2005) and Berning (2006) reported larger foraminifera (*Operculina* and nummulitids, orthophragminids, and *Heterostegina*, respectively) to co-occur with encrusting bryozoans but did not record the utilization of their tests as substratum. In a study on the taphonomy of *Nummulites*, Matteucci and Pignatti (1988) noticed borings of terebriporid bryozoans in the tests but no encrusting colonies, whereas other encrusters were present. In a Late Eocene biota from the Gulf of Mexico region, Cheetham

(1963: p. 32, table 13) noted a relationship between three bryozoan associations and the presence of larger foraminifera. However, he did not provide more detailed information on the encrusted foraminifera or on the encrusting bryozoans.

Information on organisms fouling tests of modern larger foraminifera is also fairly limited. The most detailed accounts were presented by Cook (1967, 1968a, 1968b, 1985), who noted the presence of some 50 bryozoan species on tests of *Jullienella foetida* along tropical West African coasts. This foraminifer produces flat or undulating, variably shaped tests of up to 5 cm in length. It agglutinates sand grains of a specific size-range in depths between 20 and 65 m, and is associated with sandy and muddy sea bottoms (Nørvang 1961). The foraminifer is interpreted as lying horizontally on the seafloor, although there are also indications that some tests may have grown upright being partially buried in the sediment (Cook 1985: p. 13). Both sides of the tests were usually encrusted by bryozoans. Some species (e.g., *Callopora depressa* Cook) were exclusively or mostly found on this foraminifer (Cook 1985: p. 99). Moreover, settlement experiments showed that the larvae of *Pachycleithonia africana* Cook, successfully metamorphosed only on tests of *Jullienella* when different substrata were provided (Cook 1985: p. 62), which may suggest that the larvae of certain species actively choose this foraminifer as substratum. She noted, however, that the tests are often the principal or only substratum available for settlement on an otherwise muddy seafloor (e.g., Cook 1985: p. 14). Occasionally, relatively large erect bryozoan colonies were also observed to grow on *J. foetida* (Cook 1967: p. 348, 1985: p. 15). The presence of erect colonies, as well as a possible vertical growth of the foraminiferal tests, distinguish this association from the here studied fossil lepidocyclinid/bryozoan association. Further differences are found in the composition of the encrusting bryozoan fauna (see below).

Other less detailed records include another agglutinating foraminifer from the same region, *Schizammina reticulata* Nørvang, which forms irregular thin branches instead of flattened plates as *J. foetida*, and which was less often colonized by encrusting bryozoans (Cook 1985: p. 13). The calcareous *Cycloclypeus carpenteri* from the Kei Islands (Indonesia) was found to be encrusted by 11 bryozoan species in depths between 50 and 70 m [see Cook (1968a: p. 245) and references therein]. Some of the genera encrusting *C. carpenteri* are also present on the fossil lepidocyclinids (see below). Moreover, in a study on depth distributions of living and empty tests of larger foraminifera off Japan, Yordanova and Hohenegger (2002: pl. 32, fig. 14; pl. 33, fig. 14; pl. 35, fig. 15) showed bryozoan-encrusted tests of *Baculogypsinoides spinosus* Yabe and Hanzawa, *Operculina ammonoides* (Gronowius), and also *C. carpenteri*.

Colonization by encrusting organisms occurred only on poorly preserved, reworked tests at the deeper end of the distribution spectrum of the respective species. The depth of occurrence of bryozoans on foraminiferal tests in most of the Recent associations, as well as their settlement on plate-like tests of *O. ammonoides* and *C. carpenteri*, thus contrast with the present findings from fossil associations, in which the bryozoans were exclusively found in shallow water and on undulating tests.

One potential bias affecting our study may be the sole analysis of foraminiferal tests from limestones that could easily be disaggregated. These usually contain a relatively high amount of fine-grained matrix, which prevents the limestone from excessive cementation during diagenesis. However, thin-section analysis of well-cemented limestones with lesser amounts of matrix yielded the same results: no bryozoans on tests of larger foraminifera apart from those of large lepidocyclinids.

As bryozoan larvae may actively choose the site of settlement (e.g., Buss 1979; Håkansson and Winston 1985; Bishop 1988; Ward and Thorpe 1989), the absence of bryozoans on most larger foraminifera analyzed may be explained by the absence of microhabitats suitable for settlement on certain types of tests. Alternatively, the type of environment inhabited by the foraminifera may be unsuitable for encrusting bryozoans in the first place, and/or colonies may have been destroyed by abrasion during taphonomy. These possibilities will be discussed in detail below.

The analyzed lepidocyclinid assemblage is a lateral facies equivalent of shallow-water *Porites*-Faviidae patch reefs (Schuster and Wielandt 1999; Reuter et al. 2008). Large size of lepidocyclinid tests (or angular fragments thereof), and in particular the great proportion of bryozoan zooecia that show no signs of abrasion (Fig. 4), suggest that little to no reworking has occurred. Colonization of foraminiferal tests by bryozoans is therefore very likely to have occurred in situ. Those foraminiferal tests and bryozoan colonies that are damaged rather seem to be the result of compaction of the sediment during diagenesis. The high content of fine-grained matrix in the limestone also suggests that the water was relatively turbid, which presumably prevented reef-building corals and other photophilic and/or immobile organisms, such as coralline algae, from prolific growth. A caveat is that suspended particles and higher rates of sedimentation are usually regarded as being detrimental to growth of symbiont-bearing foraminifera (e.g., Hallock 1999; but see below) as well as encrusting bryozoans (e.g., Smith 1995; Choi and Ginsburg 1983).

Bryozoans may avoid smothering by growing on undersides of bioclasts but most of the larger fragments are encrusted on both sides. This, in turn, may be explained by occasional overturning of the tests by larger benthic or

nektic organisms. An alternative explanation for the co-occurrence of encrusting bryozoans and a fine-grained matrix would be the introduction of the fine sediment to foraminiferal accumulations during storm events. Burial by obrution deposits may furthermore account for the intact bryozoan skeletons, indicating little or no reworking of the bioclasts. However, the lepidocyclinid tests are dispersed within the fine-grained limestone, whereas in obrution deposits these would be expected to occur as a concentrate (Brett 1990). In fact, other studies have provided evidence for an in situ growth of larger foraminifera in environments with a high rate of siliciclastic sedimentation (Wilson and Lokier 2002, and references therein). The extremely large size and abundance of the lepidocyclinid tests in the analyzed sample also show that environmental conditions were stable for years to decades, which may also be of importance for the high bryozoan diversity on these tests (see below).

The generation of large flattened tests within clines of foraminiferal assemblages have shown to be a response to decreased light availability or to unfavorable environmental conditions, in which case reproduction may be delayed and the test proceeds to grow (Hallock and Glenn 1986, and references therein). Coupled with an increase in size in response to decreased light availability is usually a thinning of the test (e.g., Hallock and Glenn 1986). Yet the largest lepidocyclinid tests were also extremely thick, which we therefore tentatively ascribe to continued growth not primarily related to deteriorating photic conditions. Thus, the ubiquity of fine sediment in this shallow-water setting, presumably causing turbid conditions even in moderately agitated waters, was likely to be responsible for the observed gigantism due to delayed maturation.

What further makes the present fauna special is that the tests are not only exceptionally large and thick but occasionally also extremely three-dimensional in shape (Fig. 3b). To our knowledge, there are no studies particularly devoted to three-dimensional growth in larger foraminifera, which is primarily due to the fact that lepidocyclinids with this type of growth became extinct during the Miocene. Wilson and Lokier (2002) indicated that a convex base would support the test on the soft-sediment surface. This view is supported here and expanded by suggesting that, irrespective of potential possibilities of self-extracting or -cleaning of the surface (van der Zwaan et al. 1999), undulose and especially saddle-shaped morphologies have the further advantage of forming additional, steeply inclined and exposed areas on which sediment is unable to accumulate. Furthermore, and in contrast to tests with a convex base, overturning of an undulose or saddle-shaped test results in a similar or the same upper surface topography, respectively. These lepidocyclinid tests thus seem to be an adaptation to soft-bottom environments with relatively high sedimentation rates and/or turbidity. This

interpretation is also in agreement with that proposed for Priabonian, middle-ramp, calcareous-marly packstone facies that are rich in orthophragminid foraminifera characterized by saddle-shaped tests (Bassi 2005).

One key aspect for settlement of bryozoans on large lepidocyclinids certainly lies in the very shape of their tests. The irregular undulating surface makes available a range of microhabitats while at the same time minimizing the contact area with other bioclasts. In contrast to biconvex nummulitids or plate-like heterosteginids, these larger lepidocyclinids were less likely to form a dense stacking pattern and, therefore, provided large pore space into which interstitial biota could grow. Percolation of pore water, providing the meiofauna with a steady flow of nutrients, was thereby also enhanced. Thus, bryozoan settlement and growth may not necessarily have been restricted to dead tests at the sediment surface but could also have occurred on foraminiferal tests buried by the next generation(s). Furthermore, the large size may have reduced the chances of being toppled-over by bottom currents or other organisms, while the undulating surface also provided more spatial refugia from contact point damage than that of nummulitids or heterosteginids if toppling did occur. As most of the analyzed foraminifera were, at least in some of the samples, well preserved and without any signs of abrasion, reworking as a taphonomical bias to account for the absence of bryozoans on foraminifera other than lepidocyclinids can be excluded.

A comparable modern environment in shallow tropical waters may be represented by the cryptic coral rubble habitat (Choi and Ginsburg 1983; Kobluk et al. 1988; Meesters et al. 1991). Indeed, fossil foraminiferal and Recent coral rubble associations from Caribbean reefs share some closely related species, such as *Bryopesanser pesansensis* (Smitt) and *Therenia porosa* (Smitt) (both referred to the genus *Escharina* by Kobluk et al. 1988). However, the conclusion reached by Choi and Ginsburg (1983), that interstitial sediment in coral rubble deposits has a negative impact on cavity-dwellers, is an additional feature not shared with the fossil assemblage. Another similar, though more extreme, habitat explored by bryozoans is the interstitial microenvironment of subtidal sands and gravels, in which tiny colonies encrust single grains (Håkansson and Winston 1985; Winston and Håkansson 1986; Winston and Migotto 2005). As in the coral rubble association, several genera of the bryozoan meiofauna are shared with the studied lepidocyclinid assemblage but the foraminiferal tests are significantly larger and more stable than the meiofaunal grains, resulting in the presence of different bryozoan colony growth types (see below).

#### The encrusting bryozoan fauna

Considering the rare use of larger foraminiferal tests as substrata, the occurrence of 34 taxa on lepidocyclinids of a

single sample from section Abadeh (Table 1) seems remarkable, especially because this number has to be regarded as conservative due to neomorphism of the skeleton which prohibited a more specific assignment. This number is more than twice as high as the 14 species growing on Lower Miocene lepidocyclinids from the Qom Basin, which were recorded by Furon and Balavoine (1959). Species diversities of encrusting bryozoans occurring at any one sampled site in the Recent Caribbean (Kobluk et al. 1988) or off West Africa (Cook 1968a, 1985), recorded growing on coral reef rubble and agglutinating larger foraminifera, respectively, were equal to or fewer than those of the fossil association. Likewise, the modern interstitial fauna from Florida yielded 29 encrusting bryozoan species with a potential for fossilization (Winston and Håkansson 1986).

The fauna is characterized by a comparatively great number of cribrilid species (Table 1). This is in contrast to most of the Recent associations of bryozoans on larger foraminifera or coral rubble, in which these are of relatively minor importance (Cook 1968a, 1985; Kobluk et al. 1988). Being particularly diverse at greater depths, many species of the genus *Puellina*, and also *Distansescharella*, are known to prefer cryptic and interstitial microhabitats in shallow waters (e.g., Harmelin 1988; Harmelin et al. 1989) and their abundant presence on the lepidocyclinid tests is, therefore, not surprising. Several other genera are also shared with Recent coral rubble- [*Bryopesanser*, *Disporrella* or *Patinella* (usually recorded as *Lichenopora*), *Hippothoa*, *Onychocella*, *Puellina*, *Smittoidea*, *Therenia*, *Trypostega*] and *Jullienella*-associations (*Bryopesanser*, *Callopora*, *Copidozoum*, *Disporrella*, *Onychocella*, *Therenia*, *Trypostega*, *Tubulipora*) [see Kobluk et al. (1988) and Cook (1985), respectively]. Shared bryozoan genera encrusting Recent *C. carpenteri* from the Kei Islands comprise *Bryopesanser*, *Monoporella*, and *Onychocella*, while the Floridan meiofauna also includes *Bryopesanser*, *Disporrella*, *Hippothoa*, *Puellina* and *Trypostega* (Winston and Håkansson 1986). Species of the genus *Bryopesanser* are thus present in all of the above-mentioned associations on unstable substrata, while the genera *Onychocella* and *Trypostega* (Fig. 4c) are present in at least three of these assemblages. However, as other species in these genera also occur on stable substrata and in non-cryptic habitats, there is no predictive value in the presence of these taxa per se.

Bryozoans on disarticulated bivalve shells have so far been analyzed from non-tropical environments only (Harmelin 1977; Bishop 1988, 1994; Ward and Thorpe 1989; Reguant and Mayoral 1994; McKinney 2000). The lepidocyclinid and bivalve assemblages have few taxa in common and the number of species present on bivalve shells is usually significantly smaller, which renders diffi-

cult a direct comparison. An exception is provided by large *Pinna* shells, on which, in the Mediterranean Sea, some 60 calcified encrusting bryozoans are found (Harmelin 1977). Most of the cyclostome and several cheilostome genera of the lepidocyclinid assemblage are also present on these shells. However, the greater size and stability of the *Pinna* shells also enables erect growing species to make use of this habitat.

Concerning the numbers of colonies present, population structure in the lepidocyclinid association is similar to that found in Recent bryozoan faunas on coral rubble (Kobluk et al. 1988). While 30 species show comparatively low abundances, e.g., eight species were represented by a single colony, only four species make up 50% of the total number of colonies. The anascan *Micropora* sp. (Fig. 4b) is, owing to identification problems in the similarly plentiful *Puellina* sp. 2, the single most abundant species. As predicted for colonization of small, unstable substrata, the density of bryozoan colonies is generally low and encounters rarely observed (see below). Bryozoans clearly dominate the (preserved) encrusting fauna on the tests of lepidocyclinids. Polychaete tubes and encrusting foraminifera, such as *Cibicoides* and *Placopsilina*, are only sporadically present, whereas coralline algae are absent altogether.

#### Bryozoan growth and reproductive patterns

Due to differences in, among others, modes of colony growth, encrusting bryozoans vary in their abilities in the competition for space (e.g., Buss 1979; Lidgard 1985; Bishop 1989; McKinney 1992; Taylor 1999; Okamura et al. 2001). In general, colonies of cheilostome bryozoans with multizoidal budding (*sensu* Lidgard 1985) are highly integrated and relatively superior in encounters with other organisms. Consequently, these taxa may form extensive sheets (*sensu* Bishop 1989) comprising several thousand zooids and are able to colonize and monopolize large stable substrata (e.g., McKinney and Jackson 1989). At the remaining two endpoints in Bishop's (1989) tripartite classificatory model for growth patterns in unilaminar encrusting, cheilostome bryozoans are taxa that are generally considered to be competitively inferior. The modes of growth in these bryozoans are either by zooidal or intrazoidal budding, which means that growth is slower and less coordinated, and the colonies form either spots or runners.

Presumably, as a result of their competitive inferiority, these taxa have adopted different settlement and growth 'strategies'. Species with spot colonies (Fig. 4d) are often found on substrata that have a predictable limited surface area available for colonization (such as shells or single sediment grains), as well as an inherent potential for frequent disturbance and abrasion, thereby reducing the likelihood of encountering superior competitors in this 'peripheral'

habitat. Before final settlement and metamorphosis the larvae of these species may actively search for refuges on the substrata in which chances of abrasion are minimized (Cook 1985; Winston and Håkansson 1986; Bishop 1988, Ward and Thorpe 1989; McKinney 2000). On stable substrata, spot colonies are preferentially found in cryptic habitats where competition for space with sheet colonies is similarly low due to reduced food availability (see Harmelin 1986; Okamura et al. 2001). These more or less equidimensional colonies mature early and may be of determinate size, comprising only few zooids (Bishop 1988, 1989; but see below). In contrast, uniserial runners grow strongly directional, which can be regarded as fugitive growth on spatially unpredictable substrata where competitors are present (Buss 1979; Jackson 1979), and, on certain other substrata, as a primary adaptation to growth in linear refuges or on strongly three-dimensional surfaces where obligate multiserial growth is impossible (Bishop 1989; Ward and Thorpe 1989). Between the extreme colony types sheet and spot are the moderately sized patch colonies, whereas a ribbon (pluriserial colonies with directional growth) is the intermediate growth form between sheet (or patch) and runner.

That bryozoans may form a significant part of the subtidal meiofauna in sand- to gravel-size sediments has only been discovered some 20 years ago (Håkansson and Winston 1985; Winston and Håkansson 1986), and only a single record has followed ever since (Winston and Migotto 2005). Due to the small surface provided by single sand grains, species with obligate spot colonies are present throughout these assemblages. As encrusting bryozoans were absent from smaller foraminiferal tests analyzed here, this extreme type of environment is still lacking a fossil representative. With an increase in surface area available for colonization, and the associated increase in stability of the substratum, colonies of the patch and ribbon growth types should increasingly prevail on larger substrata. Therefore, the mixture of bryozoan colony growth forms on the larger lepidocyclinid tests (see Table 1) demonstrates both meiofaunal affinities as well as elements indicative of comparatively stable conditions.

Most colonies (53%) on the tests are here considered as spots (Table 1), comprising colonies with fewer than 100 zooids. This maximum number is arbitrarily chosen and fails to consider both potentially larger spot colonies (e.g., *Cribrilina* sp.) as well as colonies that suffered death from physical disturbance (burial, overturning) before reaching their 'maximum' size (e.g., *Smittoidea* sp., Cheilostomata indet. 3–6; but see below). Fragmentary preservation is also more likely to occur in larger colonies, affecting the classification. Under stable conditions, and if the available surface area is not a limiting factor, spot colonies may continue to grow and appear as patch-type colonies. For instance,

Bishop (1994) reported a positive relationship between substratum area (i.e., stability) and colony size in *Cribrilina puncturata* (Wood), encrusting bivalve shells of different size. Thus, there is no general upper limit in zoarium size of spot colonies, and the classification of spot colonies based on the number of zooids is likely to be affected by several constraints in this assemblage.

Another feature of spots is their maturation at a small colony size, reflected by the formation of ovicells (or gonozooids in cyclostomes) during early astogeny. On the lepidocyclinid tests only a single cheilostome species, *Puellina* sp. 3 (Table 1), yielded an unequivocal pattern of an obligate spot colony, reaching maturity before formation of the 10th zooid in each colony (Fig. 4d). However, in some species Winston and Håkansson (1986) noted that, relative to conspecific colonies growing on sand grains, maturation may be delayed in colonies encrusting larger substrata (but see their p. 44 for problems with conspecificity of material from different substrata). The large area provided by lepidocyclinid tests may thus, besides enabling the colony to reach a larger colony size than on smaller substrata, promote a delay in maturity in some species. Also, due to the fragmentary preservation, ancestrulae (enabling a determination of the onset of maturation) were present in only a fraction of the larger colonies. Some colonies here classified as patches may therefore be spots.

The mode of zooid and colony growth displayed by those cheilostome species with spot colonies that encrust the lepidocyclinids is entirely of the intrazooidal type (*sensu* Lidgard 1985). The most speciose taxa contributing to this group are the Cribrilinidae (*Cribrilina* sp., *Distansescharella* sp., *Puellina* sp. 1–4) and the Escharinidae [*Bryopesanser* sp., *Escharina* sp., *Herentia* sp., *Therenia* sp. (Fig. 4e)]. The Recent sciaphile *Distansescharella seguenzai* Cipolla forms minute colonies in depths between 50 and 140 m in the Mediterranean Sea, while its Neogene representatives are interpreted to have lived in shallower water (Harmelin et al. 1989). A possible underlying trend may be supported by the presence of a congeneric species on the lepidocyclinid tests. In general, modern species of *Puellina* produce colonies of less than 100 zooids in a range of environments, including unstable substrata and cryptic habitats in shallow-water (e.g., Harmelin 1984, 1988; Harmelin and Arístegui 1988).

Similarly, the Escharinidae are usually found offshore, with only a few species occurring in shallow-water environments, where they preferentially encrust mobile bivalve shells or cryptic stable substrata, generally forming spot- or small patch-type colonies (Hayward and Ryland 1999; Berning et al. 2008). Their particular adaptation to these types of environment is exemplified by the extant *Escharina alderi* (Busk) and some other undescribed *Escharina* species (BB pers. observ.), which represent some of the

few ascophorans with a cryptocystidean frontal shield that have a uniserial mode of growth. Moreover, in his revision of the genus, Tilbrook (2006: p. 251) stated that most colonies of *Bryopesanser* species observed generally comprise of a dozen or fewer zooids, many of which were ovicellate.

The nomenclature for cheilostome colony types has here been applied also for cyclostome bryozoans. Although differing in the mode of zooid and colony formation, morphologically and functionally similar colonies are formed in this group, which allow for a comparison with cheilostomes. For instance, as in the genus *Disporella*, modern cyclostome spot colonies may be determinate in size and their larvae may actively choose the substratum type (Winston 1985; Bishop 1989; but see McKinney and Taylor 1997). Thus, some of the spot- (*Diplosolen* sp., *Disporella* sp., *Tubulipora* sp.) and runner-type colonies (*Cyclostomata* indet.), as well as both ribbon-type colonies (*Annectocyma* sp. 1, 2), are represented by cyclostome bryozoans.

Cheilostome taxa with ribbon and runner colonies are few in numbers and contribute little to covering the foraminiferal test's surfaces. Species of the two cheilostome genera with runner colonies, *Hippothoa* and *Pyripora*, are both known as fossils and are found in shallow sublittoral to outer shelf environments today (Hayward and Ryland 1998, 1999). The presence of several frontally budded, mound-like colonies (i.e., with a vertical growth component) of an unidentified celleporid bryozoan is another indication for relatively large pore spaces between lepidocyclinid tests.

Although most colonies of taxa that are here considered as patches comprise fewer than 100 zooids, the mode of zooid formation (zooidal in *Escharoides* sp. and presumably multizoooidal in *Smittoidea* sp.) and/or modern representatives of the respective genera suggest that, in general, these do not form (obligate) spot colonies. The largest colonies on the lepidocyclinid tests, which are almost exclusively preserved as fragments yet still comprising over 200 zooids, are formed by the anascan *Micropora* sp. (Fig. 4b). Although zooid formation proceeds by intrazoooidal budding, as in the spot colonies present, this species was able to cover a large area on many tests. Colony sizes of over a centimeter in diameter suggest that the tests remained in a stable position, or at least remained in a position that prevented the colony from being smothered, for a year or more. *Micropora* colonies were also the only ones encrusting strongly convex regions of the tests, such as the prominent central umbo. Whereas it is likely that extensive *Micropora* colonies have completely overgrown smaller spot colonies, thus eluding direct observation, confrontation and competition with other colonies was rarely observed (and there was no evidence that the encounter occurred when both colonies were alive). Only a tiny fraction of the area available on those lepidocyclinid tests from which *Micropora* colonies were absent was colonized at all.

In comparison with the modern bryozoan fauna on *Jullienella foetida* tests, the only other known association between larger (albeit agglutinating) foraminifera and encrusting bryozoans (Cook 1968a, 1985), the fossil fauna is generally comprised of smaller colonies. There are several species on *Jullienella* that may cover the surfaces entirely and the occupied space, even where these are absent, seems to be greater in the modern assemblage (cf. Cook 1985: fig. 2). The presence of erect colonies on *Jullienella* further shows that at least one side of the foraminiferal test was exposed and that this substratum is comparatively stable. The complete lack of erect forms on fossil lepidocyclinids, the tests of which are of comparable size, may suggest that bryozoan growth occurred in the interstitial space. However, relatively early maturation and smaller colony size in comparison with colonies from other stable substrata was also noticed in bryozoans encrusting *Jullienella* tests (Cook 1985: p. 15). Comparison between the fossil lepidocyclinid fauna and encrusting bryozoans on bivalve shells is, as mentioned above, hampered by the sole availability of information on non-tropical assemblages and the generally low number of species present on most shells. However, all of the bryozoan assemblages on bivalve shells seem to comprise a relatively greater proportion of species with multizoooidal budding compared to the lepidocyclinid assemblage, although competition for space is similarly low on most surfaces (Harmelin 1977; Ward and Thorpe 1989; Reguant and Mayoral 1994; McKinney 2000).

## Summary

This is the first study of fossil larger foraminiferal tests and their potential utilization as a substratum by encrusting bryozoans, and is, as such, rather an examination of omission. Most foraminiferal tests seem to preclude encrustations of bryozoans due to their convex (e.g., nummulitids) or flat (e.g., heterosteginids) shapes, both resulting in a dense stacking pattern with a great number of grain-to-grain contact points and reduced pore space for the meiofauna. More importantly, refuges for settlement of bryozoan larvae, which are an important feature of mobile substrata on which bryozoans are known occur, do not exist on these tests. In accordance with these facts, encrusting bryozoans were solely found on three-dimensional, undulating or saddle-shaped tests of large lepidocyclinids.

On the other hand, the presence of 34 bryozoan taxa on lepidocyclinids from a single bed shows that, once the foraminiferal substratum and environment are suitable, the tests of larger foraminifera may support a diverse bryozoan fauna. The bryozoan faunal composition, growth types and reproduction patterns on these tests combine features of both meiofaunal assemblages and those on more stable

cryptic substrata. Most genera present on the Upper Oligocene lepidocyclinids have representative species in modern-day assemblages in the interstitial habitat or on other mobile substrata such as coral rubble, larger agglutinating foraminifera, or bivalve shells. Cribrilinids form a relatively high proportion of the 34 taxa, which may indicate cryptic growth on dead foraminiferal tests at some distance to the surface, as furthermore suggested by the absence of erect growth types. The Escharinidae, as the second most abundant family, can, in general, also be considered typical for mobile substrata with a predictable limited surface and/or cryptic habitats. However, whereas species of the genus *Bryopesanser* occur in all of the faunas hitherto analyzed, there is no predictive value in their presence because other congeners may also be found on stable substrata.

Predominant mode of colony formation is by intrazoidal budding, typical for substrata on which the competition for space with other organisms is reduced, with minor contributions by species with zooidal budding. More than half of the species form spot colonies, whereas the available space provided by the large tests permitted the colonies to attain a comparatively large size and to delay maturation. Yet, only a fraction of the potential substratum is covered and competitive interactions were rarely observed. The remaining colony types include patches, ribbons and runners. Rather large colony sizes of over 200 zooids obtained by the anascan *Micropora* sp. indicate a relatively stable microenvironment.

Information on modern bryozoans encrusting foraminiferal tests and other mobile substrata is sparse; any generalizations must therefore remain premature. For instance, several lines of evidence indicate that the lepidocyclinids have lived in shallow turbid waters, whereas suspended particles were found to be detrimental to bryozoans growing on modern coral rubble. And in contrast to the present findings, flat tests of modern larger foraminifera are occasionally encrusted by bryozoans. Nevertheless, the diverse assemblage of encrusting bryozoans on these Upper Oligocene foraminiferal tests shows a long and stable history of this general type of environment and the taxa involved. Due to their abundant occurrence throughout the Oligocene and Early Miocene large lepidocyclinids may have, therefore, played a significant role in the evolution of shallow marine bryozoans by providing substrata for encrusting species in otherwise unfavorable environments. Hence, this study is an important step towards the understanding of the contribution of bryozoans to the meiofauna through time. Future research should, besides conducting essential descriptive studies of analogous modern habitats, focus on latitudinal gradients of predominant modes of colony formation by bryozoans encrusting unstable substrata, as suggested by differences in compositions between tropical and non-tropical faunas.

**Acknowledgments** The larger foraminifera were determined by Ulrike Wielandt-Schuster (Landesamt für Geologie, Freiburg). We thank Willem Renema (Naturalis, Leiden) and Elza Yordanova (Universität Wien) for discussions on larger foraminifera, and Davide Bassi as well as two anonymous reviewers for constructive criticism on the manuscript. This work was supported by the Austrian Fonds zur Förderung der wissenschaftlichen Forschung (FWF: P11886-GEO, P18189) and the Deutsche Forschungsgemeinschaft (DFG: STE 857/1-1; NE 537/1-1, -2).

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