#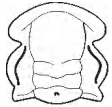 The Mediterranean bryozoan *Myriapora truncata* (Pallas, 1766): a potential indicator of (palaeo-) environmental conditions

BJÖRN BERNING

LETHAIA

Fossil and Recent specimens of the Mediterranean bryozoan *Myriapora truncata* show considerable intra- and intercolonial differences in branch diameter and zooid size. Statistically significant variability occurs within colonies, between colonies within sites, and between sampled sites, while the presence of intracolonial variability clearly shows that branch diameter is largely controlled by environmental parameters. The three structural traits measured (branch diameter, zooid size and zooid depth) do not correlate, thus indicating a disconnection between the controls on overall zooid size and branch diameter. Possible environmental parameters that may have an influence on morphology are temperature, food supply or current energy. Whereas current energy has an effect on the colony branching pattern (branch spacing), there are indications that temperature may be the main, but not the only, parameter controlling zooid size, and it is suggested that food supply largely determines the branch diameter in *M. truncata*. However, the identification of the decisive factors and quantification of the relationships between environmental and morphological change is beyond the scope of this study. The results nevertheless show that, if the control factors of morphological variability can be ascertained in Recent *M. truncata*, this species may prove to be an indicator of environmental conditions and their change at different spatial and temporal scales in Cenozoic to Recent Mediterranean habitats. □ *Bryozoa, morphology, palaeoenvironment, phenotype, variability.*

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In fossil and Recent non-tropical environments, bryozoans are one of the dominating groups of organisms regarding both species richness and carbonate production. Owing to their formation of a variety of colonial growth forms, which are more or less restricted to certain environments by physical parameters, the relative abundance of growth forms in sediments have often been used to interpret (palaeo-) environments (Stach 1936; Hageman *et al.* 1997, 1998; for a review see Smith 1995). However, relatively few studies have focused on how the environment affects intraspecific zooidal and colonial morphology, but an increasing attention is now being paid to the potential information that can be obtained from these morphological traits (e.g. O'Dea & Jackson 2002; O'Dea 2005). In colonial animals the budding of single entities, sharing the same genetic code, provides a means to establish both microenvironmental control on, and variation in, zooid morphology within a colony (Boardman & Cheetham 1969), as well as among colony variations that are environmentally and genetically controlled (Hageman *et al.* 1999). Since it has been shown that at least in some Cheilostomata the

fossil species concept based on morphotypes is valid (Jackson & Cheetham 1990), bryozoans prove to be exceptionally well suited for assessments of palaeoenvironmental conditions and their seasonal or secular changes that are reflected in the colonial and zooidal morphology of single species. Furthermore, Cheetham *et al.* (1995) suggested that, while the overall phenotype in cheilostome bryozoan species may remain morphologically rather static for millions of years, within-colony (i.e. within-genotype) variation is heritable and may play a significant part in maintaining genetic diversity in Bryozoa. Knowledge of genotype–environment interactions is therefore vital for our understanding of the evolution of clonal organisms in general.

A comparison of late Tortonian (Late Miocene) bryozoan faunas from the western Mediterranean and the eastern Atlantic Guadalquivir Basin (Fig. 1) revealed a general intraspecific difference in zooid morphology, primarily zooid size, between these regions (Berning *et al.* 2005; Berning 2006). Being the most conspicuous example due to its large colony size, fragments of the cheilostome bryozoan *Myriapora truncata* (Pallas
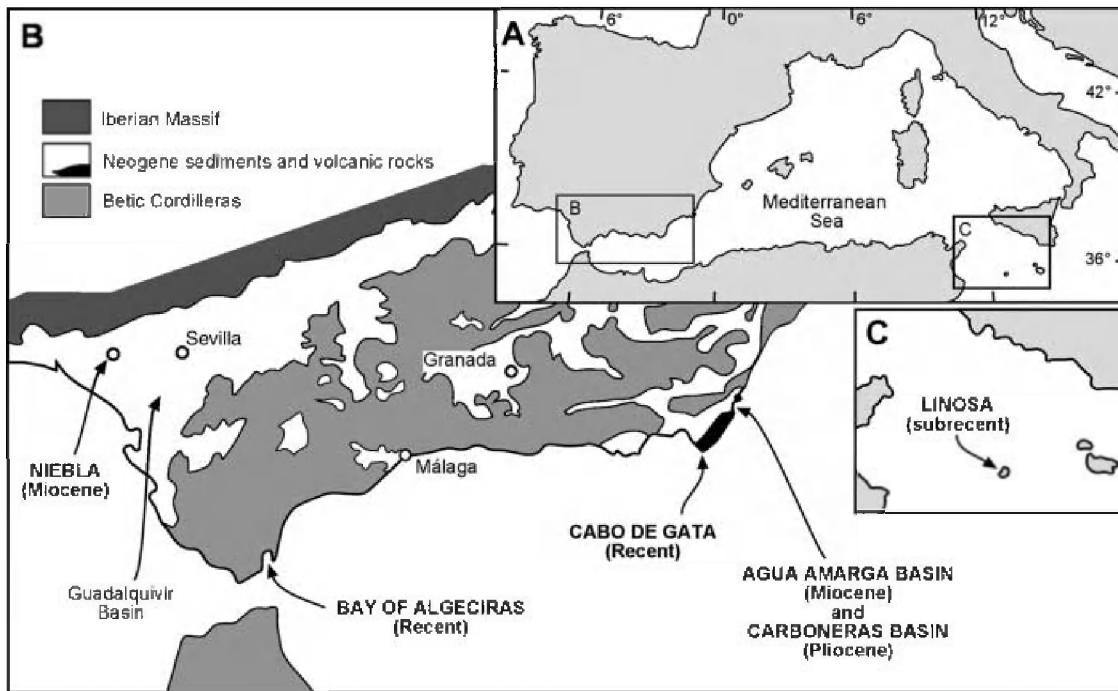
Fig. 1. Locations and ages of the sampled sites. □A. Regional map of the western Mediterranean showing position of studied sites. □B. Simplified geological map of southern Spain. Arrows indicate the studied Neogene sedimentary basins and Recent coastal sites. □C. Close-up of Linosa Island.

1766) were observed to display a significant disparity in branch diameter. Subsequent research on other fossil specimens from different localities corroborated the intracolonial and site-specific variability in branching characteristics (Fig. 2A, B) and forms the basis of the present paper. Additional material from one sub-Recent and two Recent sites was incorporated into the analysis in order to verify the presence of morphological variability in modern representatives.

Myriapora truncata has a widespread occurrence in the Recent Mediterranean Sea and a fossil record extending back to at least the Middle Miocene. Although usually reported to be endemic to the Mediterranean Sea, this species is also found on the Atlantic coasts of southern Spain and northern Morocco (Canu & Bassler 1925; López de la Cuadra & García-Gómez 1988, 1994; Alvarez 1994). Owing to its erect, robust, tree-like growth and large colony size, the 'false coral' is easily detected and identified both as a living organism and as a fossil. It grows on hard substrates such as rocks, crustose red algae and shells, and its depth of occurrence in the Mediterranean Sea ranges from the shallow subtidal, in sheltered sites such as caves, down to some 130 m (Gautier 1962; Hayward & McKinney 2002) where it occurs within the seasonally shifting shear zone of Mediterranean surface and intermediate water (A. Freiwald, personal communication 2004). Erect growth proceeds quickly after formation of an

encrusting base from a twinned ancestrula, with radiating zooids forming in more or less alternating whorls, producing a blunt growth tip. In thicker branches the space around the branch axis is filled with so-called kenozooids. These are single zooids that do not possess a polypide to feed and are usually formed for constructional reasons (Fig. 2C). All zooidal walls are perforated by numerous pores, presumably in order to minimize costs for the precipitation of calcite while at the same time attaining a rigid colony construction.

When reviewing the potential of bryozoans as indicators of water depth, Harmelin (1988) showed that, while the branch diameter seems to be unaffected, the branching pattern (branch spacing) of *M. truncata* is largely controlled by hydrodynamics. Thus, with decreasing water currents (and possibly also with increasing sedimentation rate) the length between two bifurcations increases, i.e. bushier colonies are formed in high energy environments whereas colonies in lower energy conditions are more open spaced (Fig. 2B). Although site-specific differences in branch diameter were occasionally noted by earlier authors and are known to occur in Arctic species of the genus *Myriapora* (Kluge 1975; Schäfer 1994), variability in branch diameter in relation to environmental changes has not been registered systematically in either Recent or fossil *M. truncata*. Unfortunately, in the only study available on colony growth and integration in the genus
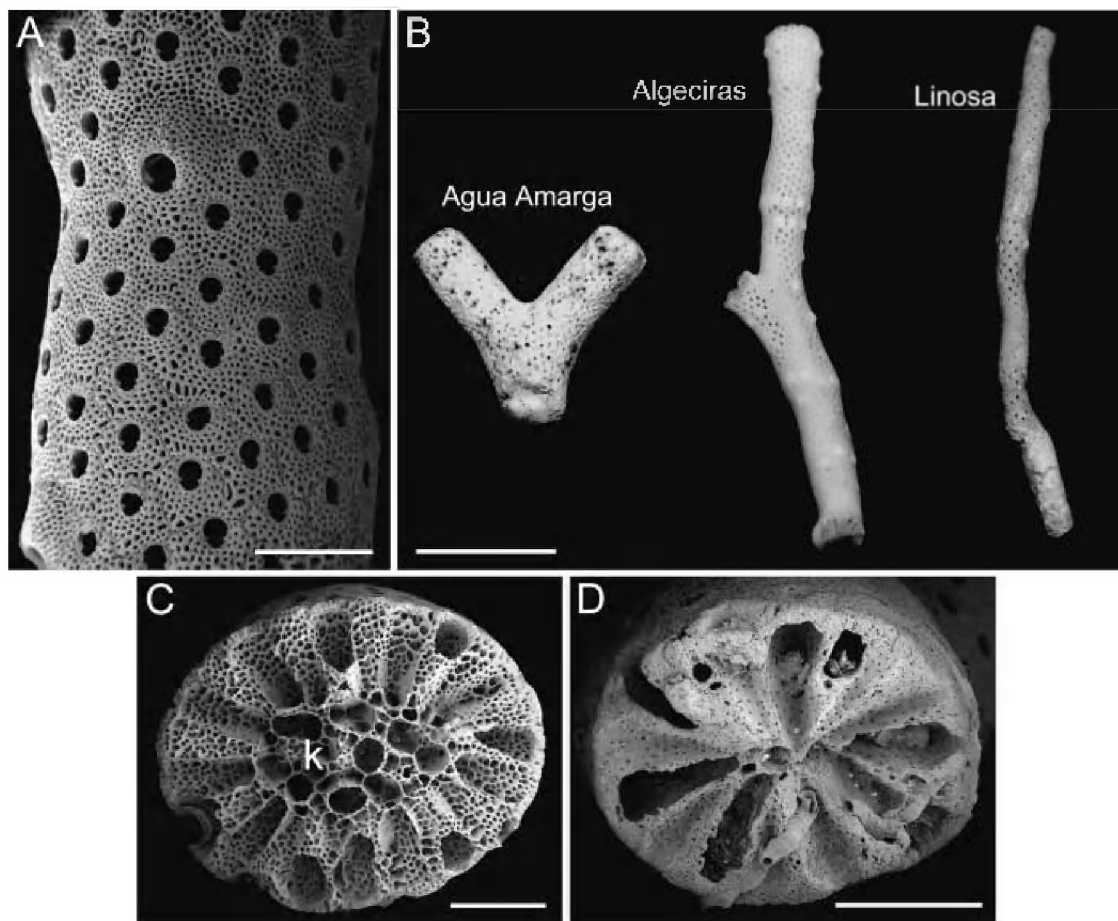
Fig. 2. Morphological and structural features of *Myriapora truncata*. □A. SEM micrograph of branch fragment from Algeciras showing perforated frontal walls, autozooecial orifices, and two ovicells at lower left and upper centre. Note the change in branch diameter. Scale bar = 1 mm. □B. Comparison of branch diameter of specimens from Agua Amarga (late Tortonian) at left, Algeciras (Recent) in middle, and Linosa (sub-Recent) at right. Note the intracolonial change in branch diameter and initial secondary calcification obscuring the orifices in proximal branch segment in Algeciras specimen, as well as differences in frequency of bifurcation: the short distance between branching points in Agua Amarga specimen (the right branch has become thicker perpendicular to paper plane and is about to bifurcate), an increased distance in Algeciras specimen (the distal tip is about to branch), and an extremely long branch fragment without bifurcation from Linosa. The elevated white dots in the Algeciras specimen are ovicells. Scale bar = 1 cm. □C. Transverse cross-section of branch from Algeciras showing the central bundle of kenozooids (k). Note the porous zooidal walls of both autozooids and kenozooids. Scale bar = 1 mm. □D. Transverse cross section of branch from Linosa. Note that not all zooids terminate at precisely the branch centre, which results in a mean zooid depth that is less than half of the branch diameter, even in the absence of central kenozooids. Scale bar = 1 mm.

Myriapora, Viskova (1986) did not include *M. truncata*. Furthermore, very little information exists about the life cycle, colony growth, or the diet of this species.

The goal of this pilot study lies in quantifying the intraspecific variation in zooid and colony morphology displayed by *M. truncata* in Recent and fossil specimens, and in demonstrating the potential this species has for reconstructing Cenozoic palaeoenvironments in the Mediterranean realm. Morphometric analysis of several structural traits will be presented to identify (1) within-colony variability, (2) between-colony variability within a certain site, and (3) among-colony variability between temporally and spatially different sample sites. Possible environmental factors controlling morphology, such as temperature, current energy, and

food supply, are discussed. The results of the present paper will hopefully stimulate, as well as serve to design future experiments on Recent *M. truncata* in order to specifically identify the causes for morphological variability in this bryozoan.

Localities studied

Fossil localities

Fossil material was collected from both the late Tortonian (Late Miocene) eastern Atlantic Guadalquivir Basin and the peripheral Mediterranean Agua Amarga Basin, as well as from the Early Pliocene Mediterranean

Carboneras Basin (Fig. 1B). The Niebla Calcarenite Formation crops out southwest of the town of Niebla in the northwestern Guadalquivir Basin. The limestone comprises coralline red algal-rich packstones to rudstones and is interpreted to have formed on a shallow shelf below fair weather wave base (Civis *et al.* 1994; Baceta & Pendón 1999; Berning 2006). The specimens of *M. truncata* from the Agua Amarga Basin derive from the Azagador Member, which is composed of bryozoan-rich, coarse-grained rudstones and grainstones (Martín *et al.* 1996; Betzler *et al.* 1997; Brachert *et al.* 1998). The sampled part of the basin hosted the carbonate factory where most of the biogenic sediment was produced by a diverse bryozoan fauna, and was situated just below fair weather wave base (Martín *et al.* 1996). During the Early Pliocene the Carboneras Basin formed a small and shallow embayment of the western Mediterranean Sea, partly overlapping geographically with the Agua Amarga Basin, in which a wide range of carbonate types accumulated (Braga *et al.* 2003; Martín *et al.* 2004). The samples were taken north of a developed spit-platform towards the current-sheltered basin centre. The above-mentioned carbonates were all formed under non-tropical conditions (rhodalgal and bryomol facies types).

Recent localities

Recent specimens of *M. truncata* were collected in the Bay of Algeciras and off eastern Cabo de Gata (Fig. 1B) by scuba-diving in about 10 m depth and from warm-temperate environments. Geographically, the Bay of Algeciras belongs to the Mediterranean; however, this region is exclusively bathed by Atlantic surface water flowing into the Mediterranean Sea through the Strait of Gibraltar. Although the depth of occurrence and general setting of these colonies are known, other environmental parameters, in order to test for potential agents governing morphological variability, were not included in this analysis because this would go beyond the scope of this work.

In addition, a grab-sample of iron oxide-stained, relict sediment from ~100 m depth off Linosa Island in the Sicily Channel (Fig. 1C) was analysed. This sample comprises numerous fragments of *M. truncata* and was taken in 1996 during RV Urania cruise 96 (sample CS96-201, 35°52′44′N, 12°50′50′E).

Material and Methods

Sampling of fossil material

The studied material from Niebla derives from two bulk samples from a thick packstone bed dominated by coralline algae (Berning 2006). Numerous specimens of *M. truncata* from the Agua Amarga Basin were collected from a single bed of the 'bedded unit' (Martín *et al.* 1996), which is mainly composed of large bryozoan bioclasts. From the Carboneras Basin, relatively large fragments of several colonies were obtained from a single floatstone bed of the Rellana de las Contraviesas sedimentary section ('middle unit' of Martín *et al.* 2004).

Characters measured and statistical analysis

From each sampled site, 25 measurements of the branch diameter were taken with a calliper to demonstrate intercolonial variation. The fragmentary nature of the fossil (and even some of the Recent) material does not permit a precise statement on the overall number of colonies (i.e. genotypes) measured. In addition, the small size of fragments usually inhibited an evaluation of intracolonial variation in branch diameter for fossil sites, with the exception of the Pliocene Carboneras Basin. Therefore, between four and six measurements only were taken from branches of a single colony per site to depict intracolonial variation. Whenever possible, measurements were taken at midpoints between two bifurcations; in case of an oval cross-section, the smallest diameter was taken to avoid measuring the lateral increase in thickness in branching regions (Fig. 3A). Furthermore, measurements were only taken in those regions of the branches where the orifices were not obscured by secondary calcification, which leads to an increase in branch diameter in older parts of the colony (Fig. 2B).

Zooidal measurements were determined with the analysis software IMAGEJ using digital SEM micrographs. Zooid depth, the distance between the frontal surface and the termination of a zooid towards the central branch axis, was measured at a transverse cross-section of a single branch per site (Fig. 3A). These measurements represent minimum values due to cross-sectional problems of the obliquely positioned and acute termination of the zooid towards the branch centre, and thus, even in the absence of central kenozooids, do not necessarily amount to half of the given branch diameter of the specific sample (see Fig. 2D).

Because individual zooid boundaries are indistinct on the colony surface, an approximation of the zooid size was obtained by measuring the distance between midpoints of orifices of adjacent autozooids (Fig. 3B). The midpoint (centroid) of an orifice was defined by the cross-point of two straight lines representing maximum orifice length and width (Fig. 3B).

For all characters measured, the arithmetic mean, standard deviation (SD) and the coefficient of variation
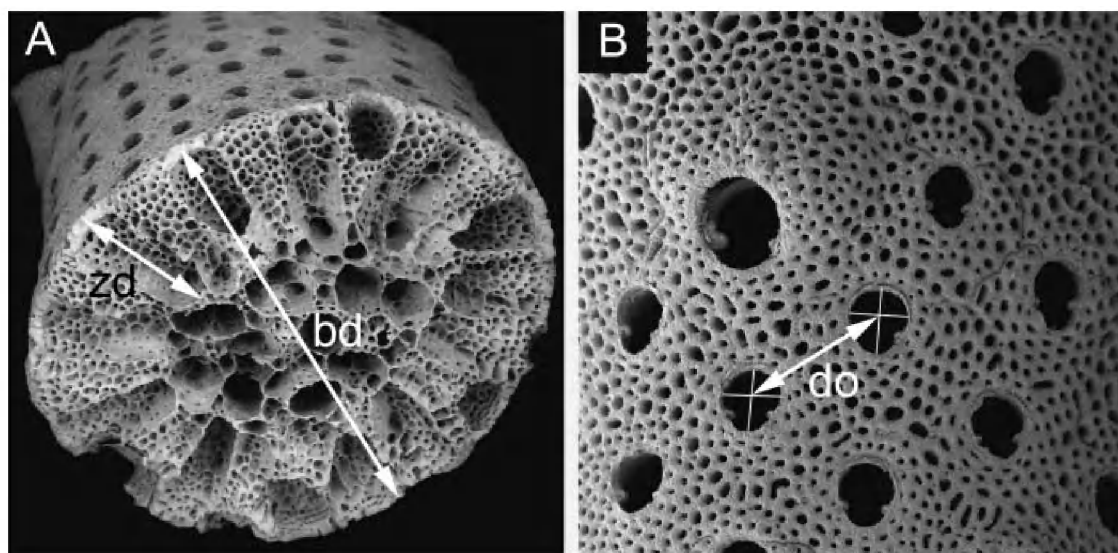
Fig. 3. Morphological characters measured in *M. truncata.* □A. Transverse cross-section of branch showing the measured characters 'branch diameter' (bd) and 'zooid depth' (zd) of the radial autozooids. Note the slightly oval cross-section of the branch and that the smallest diameter was used for the analysis. □B. Close-up of the porous frontal surface depicting the measured 'distance between midpoints (centroids) of orifices of adjacent autozooids' (do) as an approximation of zooid size. Note the ovicell with enlarged orifice at upper left.

Table 1. Intracolony variability in branch diameter (in mm) in fossil and Recent *Myriapora truncata.*

Site	Age	Mean	SD	COM	CV	Min.–Max.	n
Carboneras	Pliocene	3.3	±0.6	A	18.2	2.4–4.0	5
Linosa	Sub-Recent	2.3	±0.3	B	11.8	2.0–2.6	4
Algeciras	Recent	3.7	±0.4	A	11.6	3.2–4.4	6
Cabo de Gata	Recent	3.4	±0.4	A	12.6	2.8–4.0	6

SD, standard deviation; COM, *post hoc* Tukey's test comparison of means, samples not connected by the same letter are significantly different; CV, coefficient of variation; *n*, number of measurements made.

(CV) were calculated. One-way ANOVA and all pairs *post hoc* Tukey's tests were performed on the original measurements of intra- and intercolonial branch diameter, zooid size (i.e. the distance between midpoints of adjacent orifices), and zooid depth, using a categorical *x*-axis with sample location as a category.

In addition, the number of autozooids per whorl was counted. However, the zooids are not strictly arranged in whorls or in a perfectly alternating pattern, which makes this character difficult to determine precisely.

All fossil material as well as the measured and figured specimens of (sub-) Recent locations is stored in the author's collection. Additional material of the Recent samples is housed in the Departamento de Fisiología y Biología Animal of the Universidad de Sevilla (material from the Bay of Algeciras), in the Departamento de Estratigrafía y Paleontología of the Universidad de Granada (material from Cabo de Gata), and in the Institut für Paläontologie of the Universität Erlangen (material from Linosa).

Results

Intracolonial branch diameter

Due to the fragmentary nature of the fossil material, only a few within-colony measurements from four sites were obtained (Table 1). However, these measurements, displaying microenvironmental control on colony morphology, yielded differences between absolute minimum and maximum branch diameter ranging from as little as 0.6 mm in sub-Recent specimens from Linosa (CV of 11.8) to 1.6 mm in a sample from the Pliocene Carboneras Basin (CV of 18.2), with the latter representing an increase in diameter of some 67% (min. 2.4 mm, max. 4.0 mm). Differences in intracolonial variability in branch diameter between sites proved to be significant ($F = 7.59$, $P \leq 0.002$) and *post hoc* Tukey's test showed that the Linosa sample is significantly different from all other samples (Table 1). However, these results are based on a rather small and unequally distributed number of measurements.

Table 2. Intercolonial variability in branch diameter (in mm) in fossil and Recent *Myriapora truncata* from the various sites studied. Abbreviations as in Table 1.

Site	Age	Mean	SD	COM	CV	Min.–Max.	*n*	No. of colony fragments measured
Agua Amarga	Tortonian	4.8	±1.0	A	20.5	3.0–6.6	25	17
Niebla	Tortonian	2.7	±0.4	C	13.4	2.0–3.4	25	22
Carboneras	Pliocene	2.9	±0.4	C	15.1	2.2–4.0	25	10
Linosa	Sub-Recent	2.5	±0.3	C	13.1	2.0–3.1	25	11
Algeciras	Recent	3.5	±0.5	B	13.9	2.6–4.4	25	8
Cabo de Gata	Recent	3.3	±0.4	B	11.9	2.6–4.0	25	5

Table 3. Measurements (in µm) of the distance between centroids of orifices of adjacent autozooids as an approximation of zooid size (see text for explanation). Abbreviations as in Table 1.

Site	Age	Mean	SD	COM	CV	Min.–Max.	*n*	No. of colony fragments measured
Agua Amarga	Tortonian	616	±49	A	8.0	548–740	20	1
Niebla	Tortonian	526	±63	C	12.0	409–649	20	3
Carboneras	Pliocene	585	±76	B	12.9	449–749	20	2
Linosa	Sub-Recent	672	±75	A	11.1	568–817	20	2
Algeciras	Recent	598	±42	B	7.1	508–683	20	2
Cabo de Gata	Recent	601	±72	B	12.0	495–815	20	2

Intercolonial branch diameter

Differences in branch diameter were found to be highly significant between the studied sites ($F = 58.71$, $P \leq 0.001$). By far the largest mean diameter is displayed by specimens from the Tortonian Agua Amarga Basin (4.8 ± 1.0 mm) whereas sub-Recent specimens from Linosa have the smallest branch diameter (2.5 ± 0.3 mm) (Table 2). The measured values range from an absolute minimum of 0.2 mm (in Linosa and Niebla specimens) to 6.6 mm (Agua Amarga); the branch diameter in *M. truncata* thus varies by a factor of more than three in the available material.

Having a mean branch diameter of 3.3 ± 0.4 mm (Cabo de Gata) and 3.5 ± 0.5 mm (Algeciras), the Recent shallow-water specimens are both larger than fossil representatives from Niebla and Carboneras. However, they are still considerably smaller than late Tortonian specimens from Agua Amarga. Minimum and maximum branch diameters of 2.6 to 4.0 mm (Cabo de Gata) and 2.6 to 4.4 mm (Algeciras) are in the range observed in Pliocene Carboneras specimens. *Post hoc* Tukey's test revealed that the Agua Amarga sample is significantly different from all other sites, whereas there are no significant differences between Algeciras and Cabo de Gata, nor between Linosa, Carboneras and Niebla (Table 2).

Besides this between-sites variation, a striking contrast exists in within-site diameter variability: whereas minimum and maximum values range from 3.0 to 6.6 mm in Agua Amarga specimens (CV of 20.5), branches of the sub-Recent *M. truncata* from Linosa show the smallest absolute range of variation (2.0 to 3.1 mm, CV of 13.1).

Zooid size

Surprisingly, the specimens with the smallest branch diameter from Linosa show by far the largest mean (672 µm) and also the largest absolute value (817 µm) of distance between adjacent orifices of all measured samples (Table 3). The control factors of zooid size are thus disconnected from those governing branch diameter. However, mean values of the remaining samples more or less correspond to branch diameter values, with specimens from Agua Amarga having large zooids (616 µm) and Niebla specimens displaying the smallest mean (526 µm) and absolute (409 µm) zooid size. The great variation in absolute values in these measurements is due to structural constraints, since the distance to the orifice of a distal zooid may be considerably different from the distance to the orifice of a distolateral zooid (see Fig. 3B). However, zooid size differences between sampled sites are highly significant ($F = 10.95$, $P \leq 0.001$), whereas the sample from Niebla is significantly different from all other samples, and the sample from Linosa is indifferent only to the Agua Amarga location (Table 3).

Related to the interaction of branch diameter and zooid size, an increase in the number of zooids per whorl can be observed with increasing branch diameter. Whereas there are about six to eight zooids per whorl in Linosa specimens, Agua Amarga branches are composed of up to 16 zooids per whorl.

Table 4. Intracolony variability in zooid depth (in μm) in relation to branch diameter. Branch diameter values (in mm) were taken at the position where zooid depth was measured. Abbreviations as in Table 1.

Site	Age	Mean	SD	COM	CV	Min.–Max.	*n*	Branch diameter
Niebla	Tortonian	935	±42	C	4.5	881–988	9	2.3
Carboneras	Pliocene	967	±64	B	6.6	852–1030	9	2.2
Linosa	Sub-Recent	962	±71	B	7.4	861–1108	9	2.2
Algeciras	Recent	1058	±69	A	6.6	928–1142	9	3.3
Cabo de Gata	Recent	971	±51	B	5.3	914–1065	9	3.0

Zooid depth

In order to be able to directly relate zooid depth to branch diameter, the transverse cross-section of a single branch per location was measured (Table 4). Although differences between sites are comparatively small, they are still highly significant ($F = 5.65$, $P \leq 0.001$). *Post hoc* Tukey's test showed that the samples from Niebla and Algeciras are significantly different from Carboneras, Linosa and Cabo de Gata, and from each other (Table 4). Whereas the lowest minimum values are related to the smallest branch diameter (852 μm in the specimens from Carboneras), zooid depth does not increase arithmetically with increasing branch diameter, and maximum zooid depth was never found to exceed 1.2 mm. The discrepancy between the limited zooid depth and an increasing branch diameter is balanced by the formation of central kenozooids around the central branch axis. While these are absent in the narrow branches from Linosa (Fig. 2D) and there are only very few in specimens from Niebla, the kenozooids become more numerous in thicker branches from Cabo de Gata and Algeciras (Fig. 2C).

Discussion

Fossil and Recent branches of the cheilostome bryozoan *M. truncata* show significant variability in diameter within and between study sites as well as within colonies. Overall, a more than threefold increase in absolute branch diameter (minimum: 2.0 mm, Linosa; maximum: 6.6 mm, Agua Amarga) was observed. This discovery is in itself remarkable given the fact that in this species branch diameter variability has not been registered systematically before, although *M. truncata* is, geographically and chronostratigraphically, a well represented and often cited species in the Mediterranean region. Even though it is often recorded, a potential pitfall of this study would be the presence of cryptic species, in which case between-site and, possibly, within-site comparisons would be unfounded. However, there are indications that cryptic speciation in *M. truncata* has not occurred. The genus *Myriapora* is not very speciose, only one other species (*M. bugei*, d'Hondt 1975) is known from the Neogene to Recent in the central eastern Atlantic and Mediterranean Sea. Thus, speciation in this genus is seemingly a rare event. Furthermore, intracolonial variability accounts for a large part of the total range of variation (compare Table 1 and Table 2). It therefore seems likely that *M. truncata* is a single species with a great potential of phenotypic plasticity, which experienced stabilizing selection throughout the Neogene. Nevertheless, the presence of cryptic speciation needs to be tested on Recent representatives using genetic analyses.

Another drawback would be a taphonomic bias for larger and more robust branch fragments in the limestones from Niebla, Agua Amarga and Carboneras. However, the sampled facies of the Niebla Calcarenite consists of large fragments of coralline algal bioconstructions with varying amounts of a fine-grained matrix, and extremely delicate morphological characters are preserved (Berning 2006). Thus reworking of the clasts must have been minimal and non-selective. The calcirudite from Agua Amarga is composed of well-preserved bioclasts of a range of grain sizes, including branches of *M. truncata* showing the greatest disparity in diameter of all sites. Therefore, although some reworking did occur in this environment, it is of negligible importance in this sample as well as in the Carboneras Basin limestone, in which large colony fragments are preserved in a fine-grained matrix.

What causes the variability in branch diameter? Variations between sites and between colonies excepted (but see below), major genetic control on branch diameter is precluded because of the occurrence of significant intracolonial variability. Since all zooids of a colony share the same genetic code, a certain branch diameter would be determined early in colony formation and would not be subject to change throughout colony growth except in regions of bifurcation or secondary calcification. The triggers thus have to be of extrinsic nature.

A variety of environmental parameters have hitherto been identified that may have an effect on zooid and/or colony morphology in Recent bryozoans: among others, current energy has an influence on zooid and colony shape (Harmelin 1973, 1988; Thomsen 1977;

Okamura & Partridge 1999), zooid size is temperature-dependent (Okamura & Bishop 1988; Hunter & Hughes 1994; O'Dea & Okamura 1999; O'Dea 2005), and food availability may affect zooid size, colony growth rate and shape (Jebram 1973; Winston 1976; Hunter *et al.* 1996; O'Dea & Okamura 1999). The possible bearing of these observations on zooid and colony morphology in *M. truncata* will be briefly discussed below.

As it is likely that interactions among these environmental parameters result in a non-linear ecophenotypic response, and that the interdependence between environmental change and morphology is, in all probability, species-specific (cf. Taylor *et al.* 2007), it must be stressed that generalisations should be made cautiously.

Current energy

The amount of water movement has been found to be an important control factor on morphology in many sessile marine organisms from various taxonomic groups (e.g. Kaandorp 1999). However, whereas in most species, an increase in current energy results in the formation of thicker, more compact branches and colonies (Kaandorp 1999), branch diameter in *M. truncata* remains unaffected, as was shown by Harmelin (1988). Instead, the distance between branching points and thus the average distance between branch tips ('branch spacing'; see Kaandorp 1999) decreases with increasing water movement (and possibly also with a lowered sedimentation rate), resulting in densely spaced, bushier colonies (Harmelin 1988). Differences in branch spacing were also observed in the present study: while colony fragments from Linosa Island show long (up to 4.1 cm) branch sections without bifurcation and therefore indicate growth in a low-energy environment, colonies from the shallow-water setting from the Bay of Algeciras and, in particular, Agua Amarga are formed by more frequently bifurcating branches (Fig. 2B). The sample from Algeciras includes both relatively bushy colonies as well as longer branch segments, thus implying changing hydrodynamic conditions during colony growth. Consequently, current energy as a control factor of primary branch diameter in *M. truncata* is, if at all, of negligible importance.

Temperature

Changes in temperature are interpreted to have an impact on zooid size by controlling the solubility of oxygen in seawater (Okamura & Bishop 1988; Hunter & Hughes 1994; O'Dea & Okamura 1999). With rising temperature the solubility of oxygen decreases whereas the zooid's metabolic rate increases; thus, in order to

increase the surface/volume ratio of the bryozoan soft parts to compensate the higher oxygen demand, smaller zooids are formed in elevated temperatures (O'Dea & Okamura 1999). This inverse temperature–size effect has been applied to both Recent (O'Dea & Okamura 2000; O'Dea & Jackson 2002; O'Dea 2005) and fossil (O'Dea & Okamura 2000) bryozoan faunas to assess temperature variation, i.e. seasonality, during colony growth. However, there are two structural problems in applying the temperature–size effect to *M. truncata*: (1) lateral walls are not readily discernable on the colony surface, thus a less precise approximation of zooid dimensions (in the form of measuring the distance between centroids of adjacent orifices, see Results) must be used, and (2) unlike most other shoebox-shaped cheilostome zooids, in which zooid length and width are the largest measures and zooid depth (or height) is smallest, in this species the distance between zooid surface and termination towards the branch axis, the zooid depth, accounts for the largest zooid size parameter (compare Tables 3 and 4).

The morphometric results are, nevertheless, surprising: it is not the branches with the largest mean or maximum diameter from Agua Amarga that are constructed of zooids with the largest frontal surface but those with the smallest diameter from Linosa (Table 3). Although all other branches show a correlation, yet not a strictly linear one, of branch diameter and distance between orifices, the disparity in Linosa specimens suggests that zooid size and branch diameter are controlled by different factors. Alternatively, the increase in zooid surface area in Linosa specimens could be a consequence of its reduction in branch diameter and the associated shortening of the zooid depth, i.e. the frontal area is increased in order to volumetrically balance the loss in the zooid's third dimension. However, this scenario appears unlikely since Niebla specimens have only slightly larger branch diameters and yet have the shortest distance between adjacent orifices measured in all samples.

Compared to smaller zooids from shallow-water Recent sites, the formation of large zooids of sub-Recent Linosa specimens from an inferred deep-water and thus cooler water habitat, may reflect the inverse temperature–size effect. In turn, the presence of smaller zooids in Niebla specimens would indicate warmer temperatures in the late Tortonian eastern Atlantic compared with the larger zooids of the western Mediterranean Agua Amarga site. However, this scenario is somewhat contradictory since there are no reefs recorded from the eastern Atlantic (Esteban *et al.* 1996), whereas these thrive in marginal basins of the late Tortonian western Mediterranean, thus indicating lower temperatures in the eastern Atlantic. Although the local environment

of the Agua Amarga Basin could have been influenced by upwelling and thus cooler temperatures, which might also explain the nutrient-enriched conditions there (see below), this scenario nevertheless shows that temperature may be not the only environmental factor controlling zooid size.

As zooid size, zooid depth comprises only a limited contribution to an increasing branch diameter due to the fact that, even in thicker branches, a zooid depth exceeding ca. 1.2 mm was not observed. Instead, circum-axial kenozooids are formed which fill the residual central space around the branch axis (Fig. 2C). Their presence was already noted by Donati (1750), even before *M. truncata* was formally described by Pallas (1766), yet the nature of these irregular, vertically elongated kenozooids that are riddled with communication pores remains unexplained. Since the kenozooids are formed coeval with the surrounding autozooids, their number has to be determined during construction of each whorl. Thus, these play a vital role since the formation of an increasing number of autozooids per whorl would, due to a restricted zooid depth and without coeval construction of kenozooids, result in tubular growth with a disadvantageous terminal opening. (In fact, there is an Oligocene congeneric species, *Myriapora fungiformis* Vávra, 1983, displaying an open chalice- or chanterelle-like growth in which there are no central kenozooids, while the autozooids form an inner basal wall and open out- and downwards. However, although starting from an encrusting base and a short erect trunk (Vávra 1983), as does *M. truncata*, no branches or bifurcations are developed.) Whether or not the kenozooids fulfil any other task, such as nutrient storage, remains as yet speculative.

Food supply

Compared to the factors 'current energy' and 'temperature', little is known about the effects of quantitative changes in food supply on bryozoan zooid or colony morphology, and, even worse, the quality of food particles ingested by bryozoans is poorly understood despite the fact that it has been shown to be a factor controlling morphology (Jebram 1973; Winston 1976). Although several experimental studies showed that under optimal feeding conditions larger zooids may be formed (Jebram 1973) and the colony growth rate is increased (O'Dea & Okamura 1999), the results are inconsistent, especially regarding zooid size. For instance, in both laboratory (Hunter & Hughes 1994) and field studies (O'Dea & Okamura 1999), zooid size was controlled by temperature and genotype but was irrespective of food supply. However, since different species were studied in the above mentioned experiments the respective effects may be species

specific. Furthermore, laboratory experiments are likely not to reflect the natural environment in that, in most cases, bryozoans were fed with a monoculture of species of the flagellate algal genus *Rhodomonas*. Although representatives of this cryptophyte genus have been shown to sustain viable and reproducing bryozoan colonies during long-term studies, whereas other types of food or mixtures of various foodstuffs mostly yielded less positive results (Hunter & Hughes 1991), colony growth under laboratory conditions proceeds nevertheless substantially slower than in natural environments (Hunter *et al.* 1999; Kahle *et al.* 2003). This is not surprising, considering that a study on British coastal waters revealed over 50 different types of potential food sources available to bryozoans (Best & Thorpe 1994); thus, natural conditions, and therefore morphological reactions to varying quantity and quality of nourishment, will be difficult to reconstruct in the laboratory.

In the Recent, Arctic, congeneric species *Myriapora coarctata* (Sars 1863), Schäfer (1994) found an annual thickening of branches, in which thicker growing tips were observed in summer when the samples were taken. These thicker portions were mainly composed of feeding autozooids, whereas non-feeding avicularia dominated the thinner portions. Since temperature change is negligible at the sampled sites in these Arctic environments, Schäfer (1994) concluded that branch diameter variation may represent seasonal nutrient cycles, with phytoplankton-rich waters triggering branch thickening during summer.

A comparison of the environments of the studied sites suggests that nutrient supply may also play a role in determining branch diameter in *M. truncata*. The sampled part of the Tortonian Niebla Calcarenite is composed of photoautotroph red algal crusts and the large foraminifer *Heterostegina*, and echinoderms, whereas filter-feeding bryozoans are diverse but volumetrically of little importance (Baceta & Pendón 1999) and the branch diameter in *M. truncata* is small. In contrast, the Tortonian Azagador Member in the Agua Amarga Basin is dominated by filter-feeding bryozoans, bivalves and barnacles, as well as smaller benthic foraminifera (Martín *et al.* 1996), while *M. truncata* produced thick branches in this environment. Thus, the trophic regime, with an oligotrophic environment prevailing during formation of the Niebla Calcarenite and a relatively nutrient-enriched environment prevailing during deposition of the Azagador Member, as signalled by the faunal dominance of filter feeders, may induce the formation of smaller or thicker branches, respectively. Similarly, the differences between thicker branches from shallow-water Recent sites and the thinner branches from Linosa (Fig. 2B), which are interpreted to have formed in lower energy

and presumably deeper environments, may be due to an increased food supply in shallower waters in comparison with greater depths.

In any case, the increase in branch diameter makes possible the formation of a larger number of autozooids per whorl. This may enhance the utilization of food supply relative to colony sections with thinner branches which, in turn, may result in an increase in growth rate and, more importantly, reproductive investment. The specimen from Algeciras in Fig. 2B shows that ovicells occur abundantly, yet not exclusively, in thicker branch sections or in regions where the branch is beginning to thicken. It may therefore be likely that intracolonial (i.e. genetic) plasticity enables a morphological adaptation to short-term (e.g. seasonal) changes in food supply in order to maximize fecundity (see also Schäfer 1994). Unfortunately, the available material was not sufficient to quantify the ovicell/branch diameter relationship.

Environmental versus genetic control

Intracolonial change in branch diameter clearly provides evidence for fluctuating environmental conditions during growth. But can this finding be extrapolated to infer changing conditions in time-averaged (fossil) faunas or even between (fossil) sites several hundred kilometres apart in which cases genetic divergence has to be considered? The results of several common garden experiments and field studies suggest that, in addition to environmental factors that account for a great extent of variation within colonies, genotype creates significant morphological variation between colonies (Bayer & Todd 1996; Hageman *et al.* 1999; O'Dea & Okamura 1999). Therefore, to draw conclusions about the (palaeo-) environment from morphometric comparisons between colonies, especially in time-averaged fossil faunas, and between sites might be unfounded. A thorough statistical analysis of variation in order to quantitatively distinguish between genetic and environmental control on branch diameter within and between colonies is, due to the fragmentary state of preservation of the available fossil material, not possible and even for Recent colonies beyond the scope of this paper. However, the present study provides some indication that in *M. truncata*, intracolonial variation might comprise a large part of the absolute within-site variation in branch diameter (compare results in Tables 1 and 2). Suppose that between-colony and between-site variation were genetically controlled and that environmental conditions had a comparatively minor effect, it would be remarkable that the time-averaged late Tortonian Niebla fauna, which is composed of thin branches of homogeneous size, is so different from the more or less equally time-averaged late

Tortonian Agua Amarga fauna that consists of thick branches of inhomogeneous size. Also, in sub-Recent faunas a vertically restricted gene flow in the water column would have to be assumed for the offset between the thin branches from Linosa, in case these were formed in a deeper-water lower-energy environment, and the thicker shallower water specimens. In contrast, in shallow-water settings, a relatively uniform branch diameter is displayed in *M. truncata* from geographically distant regions, as far apart as from Algeciras to at least the Adriatic Sea (Hayward & McKinney 2002), where the branch diameter rarely exceeds 4.0 mm. These inconsistencies and, more importantly, the occurrence of intracolonial change in diameter, therefore suggest that variation in branch diameter between colonies and (fossil) sites is largely controlled by environmental parameters.

Summary

In addition to the earlier notion that branch spacing is a function of current energy, substantial variability in branch diameter and zooid size was detected in fossil and Recent specimens of the cheilostome bryozoan *M. truncata*. The specific control factors of this morphological variability must remain as yet unknown. However, if the qualitative and quantitative control on branch diameter and zooid size can be ascertained in Recent representatives using common garden experiments, environmental information may be gained at various spatial and temporal scales for Cenozoic to Recent Mediterranean habitats. Intracolonial change clearly indicates microenvironmental short-term or seasonal changes that occur during growth and within the lifetime of a colony. In Recent faunal assemblages, between-colony variation within a certain site therefore reflects the interaction of the genetic and environmental components controlling branch morphology. In time-averaged fossil sites the variation between colonies (or fragments thereof) might additionally record environmental stability or variability through time. For instance, not only do late Tortonian specimens from Niebla show a small mean branch diameter, but also a relatively minor disparity between minimum and maximum diameter, which suggest little environmental change through time in this time-averaged faunal assemblage. Contrasting two late Tortonian sites (Agua Amarga Basin and Niebla), the Agua Amarga Basin is represented by specimens with both a considerably larger mean branch diameter and CV, and therefore probably differed in absolute (micro-) environmental conditions from the Niebla site as well as differing in the rate of environmental change through time.

Whereas there are some indications that food supply and temperature may play a role in determining branch diameter and zooid size, respectively, the branch spacing of this erect robust species mostly varies with current energy, which, in case of a well preserved fossil fauna, might provide additional information for palaeoenvironmental reconstruction. The frequent occurrence of *M. truncata* in Recent and fossil environments, the ease of identifying this species as well as straightforward analytical methods aid in the applicability of these procedures also for non-bryozoologists.

Furthermore, the disconnectedness of the morphological traits zooid size, branch diameter and branch spacing within a single colony indicates differential selection pressures acting upon this species. Thus, with its long-ranging fossil record, *M. truncata* is also a well-suited species for studies on heritability of phenotypic plasticity and stabilizing selection, which is important for our understanding of the evolution of bryozoans and clonal organisms in general.

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