**Efrat Meroz-Fine · Itzchak Brickner · Yossi Loya · Micha Ilan**

# The hydrozoan coral *Millepora dichotoma*: speciation or phenotypic plasticity?

**Abstract** This article describes ecological and biological differences between two morphs of the Red Sea fire coral *Millepora dichotoma*. The species is divided into two main morphs: branching and encrusting, which were found to differ both in color and morphology. Each morph has two or more sub-morphs. A total of 372 *M. dichotoma* colonies were examined in a census at two study sites in the Gulf of Elat. Colony size and abundance of the two morphs were found to differ significantly between sites. Experimental examination of each morph's morphological plasticity revealed different growth rates and difference in growth plasticity between the branching and the encrusting morph. Most of the fragments from the branching colonies (94%) attached to experimentally placed Plexiglas substrate, compared with much less attachment by the encrusting fragments (11%). The growth form of the branching morph on the Plexiglas switched to encrusting, spreading over and covering the substrate. When the new encrusting colony reached the edge of this substrate, it started to produce tips, and returned to growth in the classic branching form. The encrusting morph did not change its growth form. Following attachment of the original fragments of the branching morph to the substrate, 8.1% of them produced new tips. When the original branches were removed, after converting to encrusting growth form, 19% of the fragments produced new tips. The capsule size of nematocysts of the two morphs was also significantly different (*t*-test, $P < 0.05$). Molecular data (ITS region) clearly demonstrate that these two *M. dichotoma* morphs differ considerably. Molecular evidence (srRNA) from the symbiotic zooxanthellae also shows a different pattern of clades in the hosts. The ecological, biological and molecular data thus attest to the two morphs being distinguishable. Contrary to previous reports, we consequently suggest that the two morphs of *M. dichotoma* found in the Gulf of Elat are actually two distinct species.

E. Meroz-Fine · I. Brickner · Y. Loya · M. Ilan (✉)
Department of Zoology,
Tel Aviv University, 69978 Tel Aviv, Israel
E-mail: milan@post.tau.ac.il
Tel.: +972-3-6408613
Fax: +972-3-6407274

## Introduction

Hydrozoan corals of the genus *Millepora* are among the major contributors of calcium carbonate skeletons on coral reefs (Edmunds 1999). Wide variability in colony morphology of *Millepora* has traditionally been viewed as a phenotypic response to variation in environmental conditions (de Weerdt 1981, 1984; Lewis 1989; Vago et al. 1998). Colonies of *Millepora dichotoma* show large variation in form across different environments. Such variability could engender expression of different genotypes adapted to different environments or expression of different phenotypes reflecting the environmental influence. Many marine sessile species from various taxonomical groups exhibit considerable morphological variation, which has frequently been suggested to be related to environmental impact, such as exposure to wave action (Stearn and Riding 1973; de Weerdt 1981, 1984; Lesser et al. 1994; Bruno and Edmunds 1997; Arsenault et al. 2001), depth (Bosscher and Meesters 1992; Beltran-Torres and Carricart-Ganivet 1993), degree of illumination (Graus and Macintyre 1982; West 1997; Muko et al. 2000), level of sedimentation (Todd et al. 2001) and nutrient supply (Smith and Palmer 1994; Barata et al. 2001).

When plastic characters are used to define taxonomic affinity, species separation and identification is often problematic (Schwaninger 1999). Thus, in order to determine species affiliation of different specimens it is important to examine how environmental conditions affect an individual's phenotype, as well as the genetic distance between individuals. Amaral (1994) and Amaral et al. (1997) showed that morphological plasticity in calcified hydroids has both genetic and

environmental components. Molecular tools are useful to distinguish between closely related species, but molecular markers alone are not always enough to make such distinctions. For example, molecular evidence indicates that the *Montastraea annularis* species complex is a single evolutionary entity, as opposed to the three commonly accepted morphological complexes of species (Medina et al. 1999).

The internal transcribed spacer (ITS) regions of the nuclear ribosomal RNA (rRNA sequences are increasingly being used for phylogenetic construction at and below the species and genus level because they can provide a spectrum of signals for phylogenetic resolution. This has already been used for plant and animal groups (Odorico and Miller 1997a), including anthozoan cnidarians (Chen et al. 1996, Medina et al. 1999).

The skeleton plasticity of *Millepora* species has long been recognized (Stearn and Riding 1973; de Weerdt 1981, 1984; Lewis 1989). Robust plate forms are found in turbulent water, delicate leafy and branched forms occur in calmer water, and encrusting forms occur at all depths (de Weerdt 1981; Lewis 1989; Vago et al. 1998).

In the northern Red Sea, the hydrozoan coral, *M. dichotoma* Forskal,1775, exhibits four main morphotypes: encrusting, delicate lace-like, leaf-like blades and robust "box-work" (Vago et al. 1998). It was suggested that the encrusting morph is always the initial mode of growth in *M. dichotoma* and may occur at all depths (Vago et al. 1998), later followed by upward growth or "apical shooting". The apical shooting is usually followed by dichotomous branching and the formation of a lace-like structure (Vago et al. 1998).

In the present study, the four morphotypes reported by Vago et al. (1998) were grouped into two main morphs differing in growth form: branching (delicate lace-like and leaf-like blades sensu Vago et al. 1998) and encrusting (encrusting and more robust "box-work" sensu Vago et al. 1998). Manchenko et al. (1993) arrived at a similar conclusion regarding branching forms of *Millepora* spp. from Vietnam. From the beginning of the study it was observed that the morphs also have different colors: the branching morph is brown-yellow, while the encrusting morph is yellow-green.

In this study, we compared the ecological, biological and molecular characters (the hydrozoan ITS sequences and zooxanthellae clade analysis) between the two main morphs of *M. dichotoma*. These characters were used to compare and determine whether the variability within and especially between morphs is a result of phenotypic plasticity or, rather, that they represent separate species.

## Materials and methods

### Study site

The study site was at the coral reefs in the Gulf of Elat in the northern Red Sea. Two reefs were chosen: the northern section of the Nature Reserve coral reef (NR) ($29°30'$N, $34°55'$E), which is a fringing reef of 1–3 m depth; and a site in front of the Marine Biological Laboratory station (MBL) of the Interuniversity Institute, composed of a moderately sloped profile, 0.5–15 m deep.

### Distribution and abundance of the different *Millepora dichotoma* morphs

Line transects (10 m each) were conducted at both study sites to record abundance and distribution of *M. dichotoma* colonies. The transects (five transects/depth) were carried out at the MBL site at 1, 3, 5, 7, 10 and 15 m depth. At the NR site, transects were done only at 1 and 3 m (shallow fringing reef), since at other depths the substrate is sandy and does not enable larval settlement. In each transect, the number of specimens was recorded. The two longest axes perpendicular to each other were measured for encrusting colonies and similarly for the branching morph (at the branched part). Nested ANOVA was conducted (after transformation of $\sqrt{X+0.5}$) to examine whether morph abundance was depth and/or site dependent. Nested ANOVA for size was conducted following log transformation.

### Growth plasticity and growth rate

We experimentally studied induction of plasticity in *M. dichotoma* at the MBL site at 6 m depth. For this purpose, we examined whether *M. dichotoma* fragments can change their growth pattern from encrusting to branching and vice versa, as suggested by Vago et al. (1998). A transparent Plexiglas plate was connected vertically to a horizontal elongated plastic base, to which cloth-clips were attached at 5 cm intervals (Fig. 1). The position of the clips was designed to hold *M. dichotoma* fragments at their base (the broken end), while the growing apical tips touched transparent Plexiglas squares of three sizes: small (1 cm$^2$), medium 4 cm$^2$) and large (16 cm$^2$), glued to the vertical plate ($n=9$ for each size).

The new encrusting coverage of the *M. dichotoma* over the vertical plates was photographed every 2–4 weeks, for 3 months. The coverage area was then measured using an image analyzer (Olympus CUE-3).

**Fig. 1** A construction for studying growth plasticity and growth rate of *Millepora dichotoma*. A transparent Plexiglas plate (*b*), was connected vertically to a horizontal elongated plastic base (*a*), to which cloth-clips were attached at 5 cm intervals. Transparent Plexiglas squares of different size classes $C_{1–3}$ were attached to the vertical plate
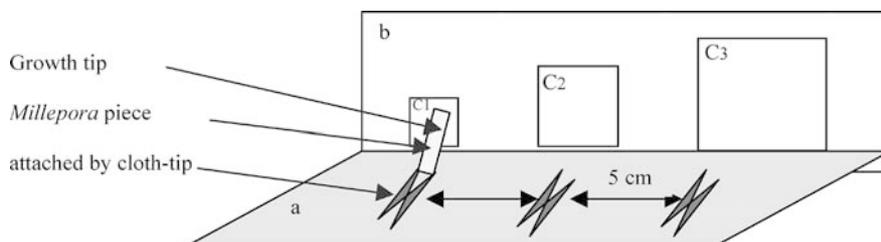
In 21 cases, following the detection of *M. dichotoma* growth on the Plexiglas plates, the original fragment was removed in order to monitor the fate of the remaining tissue growth on the plates without contact with the original fragment.

A chi-square test was conducted to determine whether growth plasticity of the two morphs is different. A Fisher exact test was performed to examine if the original branch affects growth plasticity.

### Nematocysts

To record morphological parameters of the nematocysts, it was necessary to isolate them from the tentacular ectodermal layer and to trigger their expulsion from the capsules. Triggering was carried out by immersing a colony fragment in diluted acetic acid. Following such nematocyte discharge, cysts were filtered using 22 μm millipore filters. For ultrastructural analysis of discharged nematocysts, the filters containing nematocysts were fixed for 2 weeks in 2.5% gluteraldehyde, at 4°C. Following dehydration in upgrading ethanol solutions (2.5–100%), the nematocysts were critical-point-dried, sputtered with gold and viewed by electron microscope JSM-840A (Jeol). The capsule and shaft length were measured from the photographs.

### Animal collection, DNA extraction, amplification and sequencing

Fragments of *M. dichotoma* morphs were collected off the MBL site in shallow (2–3 m; $n = 9$) and deep (10–15 m; $n = 8$) water. DNA extraction followed the protocol of Sambrook et al. (1989). Total cellular DNA was extracted from the colonies' soft tissue (removed from the skeleton by a surgical blade), and homogenized in lysis buffer. The lysate was digested for 3 h by proteinase K (25 μg/ml) at 65°C and extracted twice with phenol:chloroform (1:1). Nucleic acids were not precipitated with ethanol.

The polymerase chain reaction (PCR) was employed to amplify a fragment of the ITS region (Takabayashi et al. 1998). Primer A18S (GATCGAACGGTTTAGTGAGG), when paired with primer ITS-4 (TCCTCCGCTTATTGATATGC), amplified a single fragment. Amplification was carried out using 1 unit of *Taq* (SRP-801, JMR holdings), 2.5 mM MgCl$_2$, 0.1 mM of each dNTP, 60 pmol of each primer, and 100 ng DNA. The amplification consisted of initial denaturation at 94°C for 2 min, followed by 30 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 2 min and elongation at 72°C for 3 min. The cycles were followed by a final elongation step of 72°C for 5 min.

Direct sequencing was performed on an ABI 377 automated sequencer. Sequences were aligned using ClustalV software, followed by manual editing. Maximum likelihood analyses were performed using fastDNAml 1.0 (Olsen et al. 1994) with global rearrangement, with a transition/transversion (Ti/Tv) ratio of 0.979. Sequences obtained during this work have been submitted to the EMBL database and have been assigned the accession numbers AJ515045 to AJ515061.

The sequence of *Millepora exaesa* (Odorico and Miller 1997b) alignment was used as an outgroup (GenBank, accession no. U65484).

### Zooxanthellae phylogenetic analysis

Zooxanthellae DNA extraction followed Rowan and Powers (1991), or utilized chelex 100 resin (BioRad), as described in Veron et al. (1996). Small subunit ribosomal RNA (ssRNA) genes were amplified from total nucleic acid samples using one universal primer, ss5 (5'-GGTTGATCCTGCCAGTAGTCATATGCTTG-3'), and zooxanthellae-specific primers ss3Z (5'-AGCACTGCG-TCAGTCCGAATAATTCACCGG). Amplification and restriction followed Rowan and Powers (1991). A parsimony tree was generated by a matrix of coding each line on the agarose gel: an individual with a line got 1, an individual without a line got 0.

## Results

### Distribution and abundance of *Millepora dichotoma*

During the survey 372 colonies were observed in the studied sites. A Nested ANOVA was performed with morph nested in depth and depth nested in site. Abundance of the two morphs and size of colonies were found to differ significantly with morph nested in depth (Nested ANOVA, abundance: $P = 0.008$, $F = 3.24$, $df = 6$; and size $P = 0.0001$, $F = 5.182$, $df = 6$). Colony size also differed significantly between study sites (nested ANOVA, $P = 0.05$, $F = 151.27$, $df = 1$).

The encrusting morph at the MBL site constituted almost two-dimensional colonies, with a very thin skeleton (0.5–1 mm thick). These colonies frequently featured projections, 1–10 cm tall (Fig. 2). The branched morph at the MBL site appeared as small colonies, generally consisting of only one or two branches, growing upright, with no anastomosis growth pattern. At the MBL site this morph (identified by its color) sometimes appeared as encrustation over the substrate, usually on boulders. At the MBL site the encrusting morph was most abundant in shallow water (1 m depth) with $13.4 \pm 4.2$ individuals/10 m, and less abundant in deeper water, with $1.8 \pm 1.0$ individuals/10 m at 15 m depth (Fig. 3A). Maximal abundance of the branching morph was at 7 m depth, with $5 \pm 1.2$ individuals/10 m (Fig. 3A). The mean colony size of the encrusting morph was similar for all studied depths. In contrast, the mean colony size of the branching morph was higher at 5 and 15 m depth, being $61 \pm 58.1$ and $60 \pm 104.3$ cm$^2$, respectively (Fig. 3B).

At the NR site the encrusting morph was less abundant, and the highest density found was $5.8 \pm 2.4$ individuals/10 m at 3 m depth. The branching morph was most abundant at the NR site at 1 m depth, with $9 \pm 6.2$ individuals/10 m. Concerning colony size, the largest branching colonies were at 1 m depth, while the largest encrusting colonies were found at 3 m depth (Fig. 4).

Compared with encrusting colonies from the MBL site, the colonies from the NR site were much more massive, with larger (higher and wider) projections. The branching colonies in the NR site were also more massive than those in the MBL site, and most of the gaps between their branches were closed. Both plates and branches were thicker than in the morph colonies from the MBL site. The latter colonies had one or a few parallel, delicate, erect plates attached to the substrate through an encrusting base. Each plate was composed of dichotomous branches, which had often anastomosed and left open gaps between interlacing branches.

**Fig. 2** The encrusting (**A–C**) and the branching morph (**D–F**) of Red Sea *Millepora dichotoma*. **A** Encrusting morph, Marine Biological Laboratory station (MBL). **B** Encrusting morph with projections, MBL. **C** Encrusting morph, Nature Reserve coral reef (NR). **D** Branching morph, MBL. **E** Lace-like branching morph, NR. **F** Robust "box-work" branching morph, NR
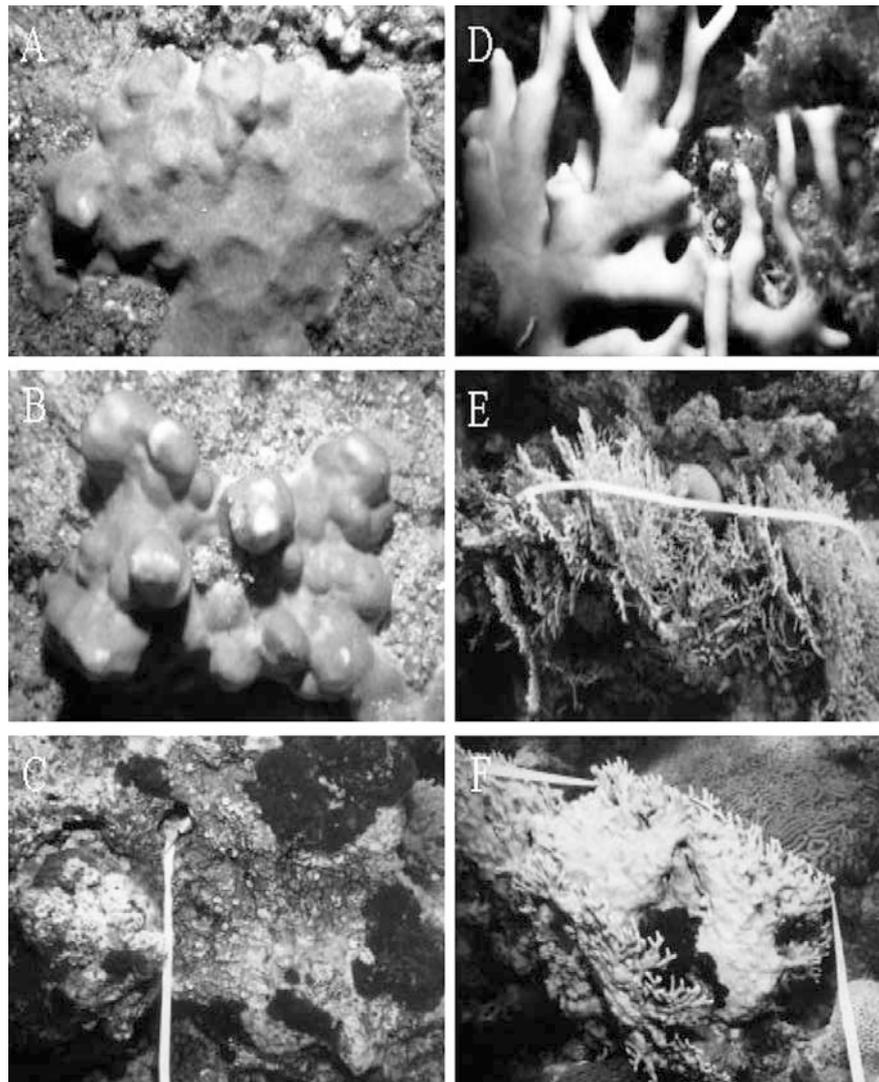


### Field experiments

*Growth plasticity of the branching morph*

Nearly all (94%) of the branching fragments attached with their tips to the substrate, their tissue growing thereon ($n=49$). Upon attachment, fragments of the branching morph changed their growth form to an encrusting appearance and began to cover the given substrate (Plexiglas plates). The large and the mid-sized plates were covered to a great extent with new *M. dichotoma* growth, while the smallest plates became completely covered. When the new growing encrusting colony reached the edge of the plate, it started to produce new tips. This was again a change in the growth form of the same colony, which led to the reappearance of the typical branching morph. These new tips appeared only at the edge of the Plexiglas plates, with or without the original fragment. There was no correlation between the new colony size on the plate and its growth pattern. The new encrustation always produced tips at the edge of the plate regardless of plate size; i.e. a *M. dichotoma*

colony that reached the edge of the Plexiglas produced new tips.

When the original branch remained attached, 8.1% (3/37) of the fragments produced new tips. However, when the original branches were removed, 19% (4/21) of the fragments developed new tips (non-significant, Fisher exact test). During the first three weeks the growth rate of the encrusting area produced by the branching morph was very high, about 6 mm²/day, reaching $130 \pm 73$ mm² after 21 days.

*Growth plasticity of the encrusting morph*

The plasticity in growth form of the encrusting morph fragments was found to differ from that of the branching fragments. Of the 170 fragments used (from different colonies), only 11% ($n=20$) attached and grew on the substrate, compared with 94% of the branching morph fragments ($P > 0.005$, chi-square test). Therefore, no manipulation (removing the fragments from the Plexiglas plates) was performed with this morph's fragments after
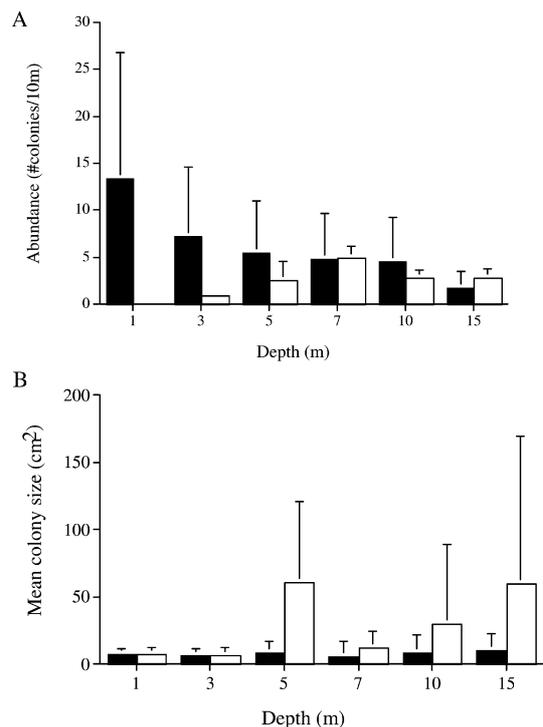
**Fig. 3A, B** Abundance and mean size of *Millepora dichotoma* encrusting and branching morphs at MBL. **A** Abundance of morphs. **B** Mean colony size. Black bars—Encrusting morph, white bars—branching morph. *n* = five line transects at each depth
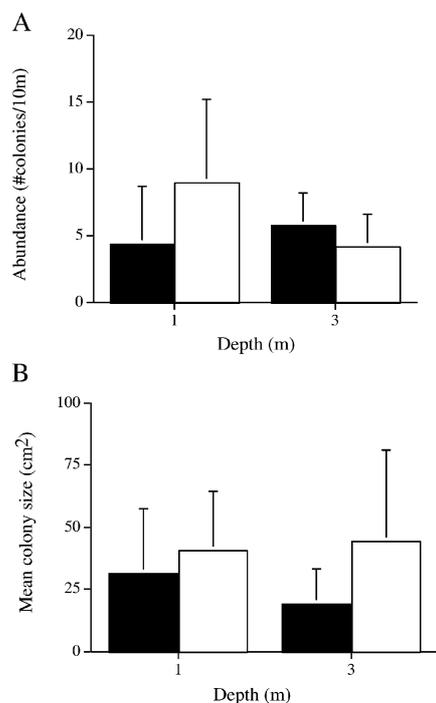


**Fig. 4** Abundance and mean size of *Millepora dichotoma* encrusting and branching morphs at NR. **A** abundance of morphs. **B** mean colony size. Black bars-encrusting morph; white bars-branching morph. *n* = five line transects at each depth

growth had started. None of the new growing encrusting colonies produced tips.

The growth rate on the plates by the encrusting morph during the first 2 weeks was 17.4 mm$^2$/day, reaching a maximal coverage area of $244 \pm 106$ mm$^2$ within this time period.

### Nematocysts

The nematocysts are of the macrobasic mastigophores type (Mariscal 1974). The capsule size of nematocysts taken from the two morphs differed significantly (*t*-test, $P = 0.027$, $t = -2.515$, $df = 12$). The length of the nematocyst capsule of the branching morph was 23.3 µm $\pm 1.6$ ($n = 11$) while that of the encrusting morph reached 25.5 µm $\pm 1.1$ ($n = 4$). The two morphs also differed significantly in the length of the tubule between capsule and barbs, being 211 µm $\pm 49$ ($n = 5$) and 62.2 µm $\pm 6.4$ ($n = 5$), in the encrusting and branching morphs, respectively (*t*-test, $P = 0.0002$, $t = -6.673$, $df = 8$); (Fig. 5).

### DNA sequences

Fragments of the ITS rDNA were amplified from branching and encrusting morphs. ITS4 regions varied in size from 900 bases in the encrusting morph to 800 bases in the branching morph. The base composition for the sequences of the ITS region was A = 28.5%, C = 21.2%, G = 20.8%, T = 29.5%. In the constructed phylogenetic tree, seven specimens of the branching morph and ten of the encrusting morph were clustered significantly into two monophyletic groups ($P < 0.01$) (Fig. 6). The average sequence divergence between morphs, calculated using the Tamura-Nei distance, was $11.9 \pm 2.9\%$. The average divergence within morphs was $3.7 \pm 6\%$ in the branching morph, and $4.5 \pm 3.4\%$ in the encrusting morph.

### Zooxanthellae clade analysis

Zooxanthellae ssRNA genes were successfully amplified from all samples and a single PCR amplification product of ca. 1,700 base pairs was obtained from each specimen. The application of restriction enzymes on specimens of the branching morph from shallow and deep water resulted in the same restriction pattern. In contrast, the restriction map of the encrusting morph differed between specimens from shallow and deep water (Fig. 7). The most parsimonious tree showed that the genotype of zooxanthellae from specimens from the encrusting morph in shallow water is the same as the genotype of those from the branching morph, but different from those isolated from deep water encrusting colonies (Fig. 7).

## Discussion

Morphological variation in *Millepora* spp. is generally believed to represent a developmental response to

**Fig. 5A–D** Nematocysts of *Millepora dichotoma*. **A** Nematocysts of the branching morph. *c* Capsule, *t* tubule. **B** Barbs of nematocysts in the branching morph. **C** Nematocysts of the massive morph. **D** Barbs of nematocysts in the encrusting morph
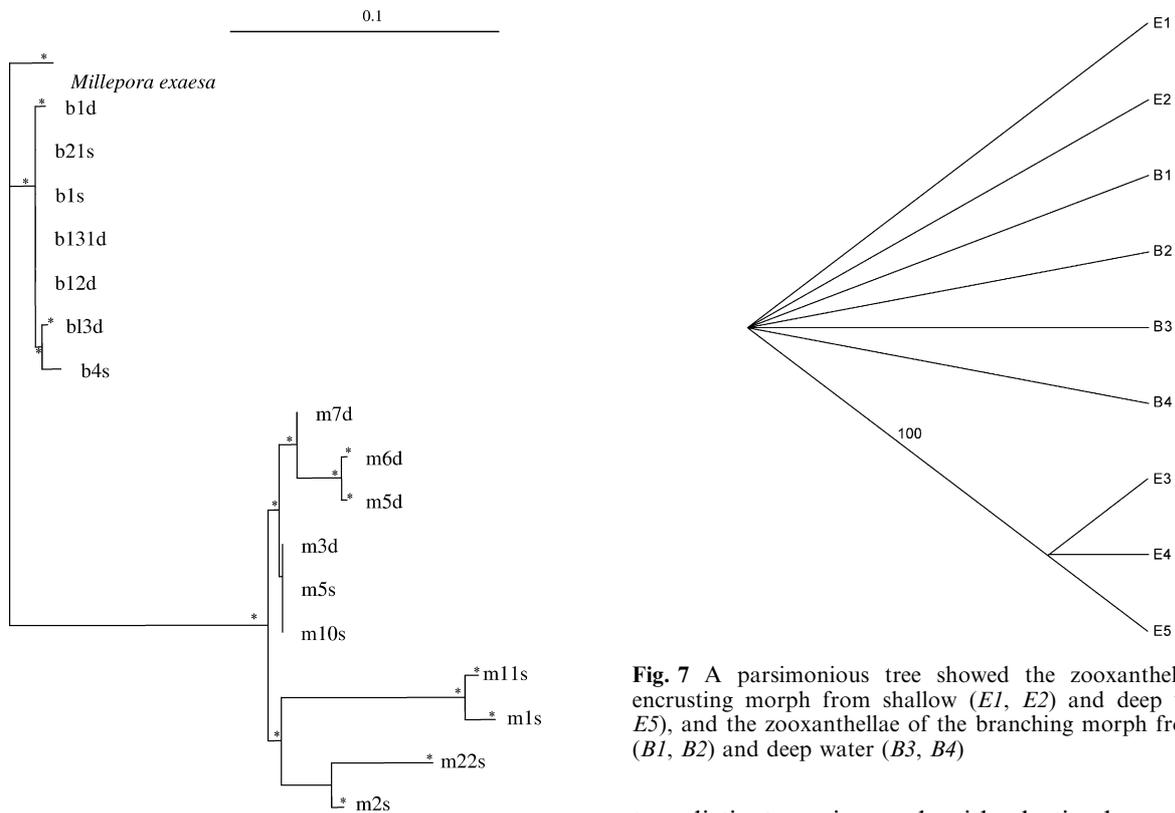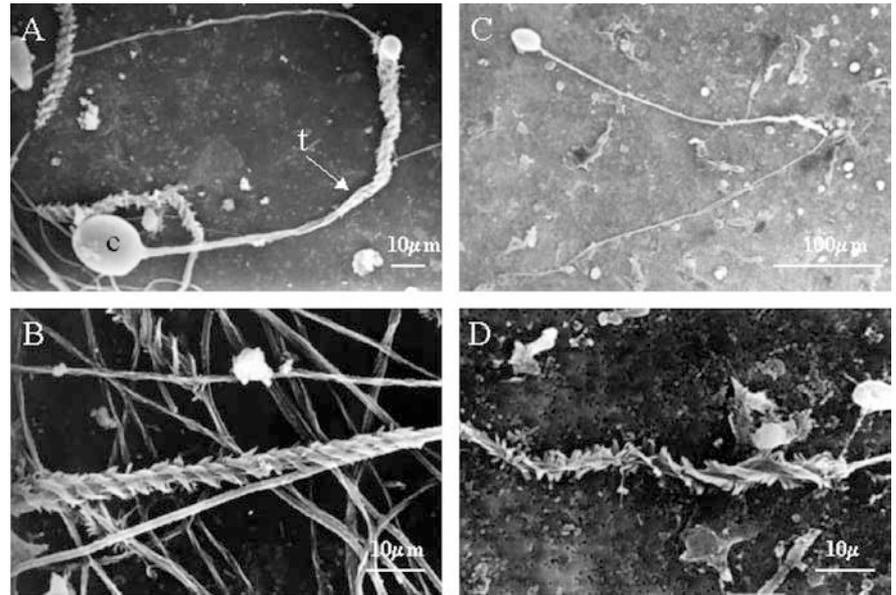




**Fig. 6** A reconstruction of the phylogenetic relationships between the encrusting and the branching morphs of *Millepora dichotoma* and *M. exaesa*. *e* Encrusting morph, *b* branching morph, *s* shallow water, *d* deep water. * represents significant differences; *scale bar* represents expected numbers of substitutions

**Fig. 7** A parsimonious tree showed the zooxanthellae of the encrusting morph from shallow (*E1*, *E2*) and deep water (*E3–E5*), and the zooxanthellae of the branching morph from shallow (*B1*, *B2*) and deep water (*B3*, *B4*)

environmental variables (Boschma 1948; Stearn and Riding 1973; de Weerdt 1981, 1984; Lewis 1989; Vago et al. 1994, 1998). Our current findings, based on ecological, biological and molecular characters from two morphs of Red Sea *M. dichotoma*, suggest that they might be two distinct species, each with plastic characters. Both morphs are plastic in their morphology and were found to differ significantly in size between study sites and depths. The branching morph was found to be much more plastic than the encrusting morph, changing its growth form from branching to encrusting and back to branching. The branching morph was found to be smaller and more delicate at the MBL site than at the NR site. Also in the encrusting morph the colonies and their projections were smaller at the MBL site than at the NR site. The differences in distribution and growth

form found in the present study within and between sites suggest that different environmental/mechanical factors (e.g. turbulence, water movement) play a role in controlling the morphological expression of each morph. Boschma (1948) emphasized that each *Millepora* species has a typical growth form that may be modified by local conditions but which reflects the colony position on the reef. The author concluded that each species can adjust to suboptimal conditions, resulting in a limited change in the colony's form (Boschma 1962). In deeper, calmer water, de Weerdt (1981) found that branching forms appear, while sturdy forms are found in more turbulent water and encrusting forms in turbid as well as in extremely turbulent places. In the present study both examined morphs were found in a range of depths with different abundance. Vago et al. (1998) assumed that the four morphs (encrusting, lace-like, leaf-like and robust "box-work") found in the Red Sea are of the same species and suggested a model for development of *M. dichotoma* in which each of the different growth forms is a stage in a sequential development of the colony's architecture. This sequence starts with the encrusting growth form and, depending on the governing environmental factors, may remain encrusting or develop towards one of the other growth forms. In contrast, in the present study we found that in the NR the distribution pattern of the branching and encrusting morphs did not correspond to the suggestion of Vago et al. (1998). For example, the abundance of the branching morph was higher than the encrusting one at 1 m compared with 3 m, although wave motion and turbulence are much stronger at the shallower depth. In the field experiment, the branching morph changed its erect growth form to an encrusting one and then back to a branching form. In contrast, the encrusting morph never changed its growth form to produce branches. Moreover, the significant difference in attachment capability (94% and 11% in the branching and encrusting morphs, respectively), under the same environmental conditions (field experiments), in addition to significant differences in nematocyte size, strengthen our hypothesis that the described *M. dichotoma* morphs are two distinct species.

The molecular data further support the biological and ecological evidence of two distinct species. The phylogenetic tree clearly demonstrates that the two morphs of *M. dichotoma* differ considerably. The ITS region shows that interspecific divergence among the two morphs of the hydrozoan is much higher than intraspecific polymorphism. Moreover, the analysis reveals that the branching morph turns out to be closer to *M. exaesa* than to the encrusting morph. One of the advantages of using ITS regions in a phylogenetic study is that the length of sequences for each of the regions is less than 1,000 bp in plants and animals. This advantage renders the ITS region relatively easy for use with PCR and sequencing (Chen et al. 2002). Our finding in the two hydrozoan morphs fits this categorization, the ITS length of the branching morph is 800 bp, and for the encrusting morph it is 900 bp.

The zooxanthellae that are symbiotic with *M. dichotoma* show a different pattern of clades in the host. The branching morph has a single clade of zooxanthellae in both deep (10 m) and shallow (2 m) water. Unlike the branching morph, the encrusting one in deep water has a different clade of zooxanthellae than in shallow water (Fig. 7). The usual assumption is that corals harbor only

**Table 1** A comparison of characters of *Millepora dichotoma* between different morphs

|  | Encrusting morph | Branching morph |
| --- | --- | --- |
| Growth form | Nearly two dimensional colonies, sometimes with projections. | Small and delicate colonies; vertical and dichotomous branches; robust massive forms. |
| Growth plasticity | Encrusting growth only | Erect growth changed to encrusting, and back to branching form |
| Growth rate over experimental plate | 17.4 mm$^2$/day | 6 mm$^2$/day |
| Field abundance | The two morphs are significantly different when nested in depth (Nested ANOVA, $P = 0.0001$) | |
| Size | Size of colonies differed significantly with morph nested in depth, and between study sites (nested ANOVA, $P = 0.05$) | |
| Nematocysts | Capsule size $25.5 \pm 1.1$ μM<br>Tubule length $211 \pm 49$ μM | Capsule size $23.3 \pm 1.6$ μM<br>Tubule length $62.2 \pm 6.4$ μM |
| DNA sequence divergence | $4.5 \pm 3.4$ within morph<br><br>Sequence divergence between morphs $11.9 \pm 2.9\%$<br>The branching morph closer to *M. exaesa*, than to the encrusting morph | $3.7 \pm 6\%$ within morph |
| Zooxanthellae | Colonies from shallow and deep water have different clades of zooxanthellae | Colonies from shallow and deep water have the same clade of zooxanthellae |
| ITS length | 900 bp | 800 bp |

one symbiont. Rowan et al. (1997) found that the Caribbean corals, *Montastraea annularis* and *M. faveolata* can host several species of *Symbiodinium* (i.e. zooxanthellae).

Other common symbionts in *Millepora dichotoma* colonies are barnacles (Mokady et al. 1999). The sequences of the 12S mitochondrial rDNA of *Savignium milleporum* barnacles collected from the same two morphs of the Red Sea *M. dichotoma*, differ considerably (Mokady and Brickner 2001). The maximum within-population pairwise sequence divergence observed was 1.6% and 1.1% for barnacles from encrusting and branching morphs, respectively. In contrast, the average pairwise sequence divergence between barnacles from the encrusting and the branching morphs was considerably larger ($>9\%$).

Table 1 summarizes the differences between the *M. dichotoma* branching and encrusting morphs, as found in this study. We suggest that these differences indicate the existence of two separate species within the present Red Sea *M. dichotoma*.

We have shown that the capability to alter morphology is very important to individuals that may grow under variable conditions in different environments, widening the options for settlement and survival in such environments. The study of patterns of ecological, physiological and genetic variation within species can thus provide insights into the process of speciation.

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