Zoological Studies **39**(3): 179-190 (2000)

Zoological Studies

A Taxonomic Reappraisal of *Montipora digitata* Based on Genetic and Morphometric Evidence

Ben Stobart*

Department of Marine Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia

(Accepted February 25, 2000)

Ben Stobart (2000) A taxonomic reappraisal of *Montipora digitata* based on genetic and morphometric evidence. *Zoological Studies* **39**(3): 179-190. Recent molecular and reproductive studies have demonstrated that 2 morphs of *Montipora digitata* are different species. In this study, skeletal morphology was examined to determine whether the species can be identified using traditional taxonomic methods, and to establish suitable names for the species. Univariate and multivariate analyses based on 5 skeletal characters revealed that the 2 species do differ in morphology. However, overlap of these characters renders them unsuitable for species identification. A further character, septal shape, was found to be species specific. Examination of museum specimens using septal shape to distinguish the species revealed that the 2 species correspond to the holotypes for *M. digitata* (Dana 1846) and *M. tortuosa* (Dana 1846). This study highlights the usefulness of a multiple-technique approach to coral taxonomy, with each alternative technique acting as a test for the other, which reduces the chance of an erroneous conclusion.

Key words: Coral, *Montipora*, Taxonomy, Morphometrics.

It is widely recognized that the high degree of intra-specific variability in skeletal morphology exhibited by scleractinian corals complicates their taxonomy. In view of this, it has been suggested that new methods be adopted to classify those coral species not easily distinguished by their morphology (Lang 1984). Furthermore, it has been suggested that several techniques should be used simultaneously to best identify species limits within the scleractinia (Willis 1990). Molecular techniques have proven to be the most popular for solving taxonomic problems within the scleractinia. Such techniques are not subject to environmentally induced variations that can affect skeletal characters, and they can demonstrate reproductive isolation which is considered proof of species status by most taxonomists (Eldredge 1993). To date, several studies have shown that the traditional approach to coral classification based on qualitative observations of skeletal morphology is in agreement with classification based on molecular techniques (Willis and Ayre 1985, Ayre and Willis 1988, Ayre et al. 1991, Van-Veghel and Bak 1993, Garthwaite et al. 1994, Lopez et al. 1999). However other studies have shown that some species may not be detected using traditional methods (Knowlton et al. 1992); species defined using traditional methods may not always be detected easily using molecular techniques (e.g., the *Montastraea annularis* complex, Lopez and Knowlton 1997, Lopez et al. 1999); and morphologically defined species may not always represent good "biological species" (Miller 1994, Miller and Babcock 1997). These inconsistencies highlight the need to further explore the relationship between morphological and "biological" distinctness in the scleractinia using multiple techniques.

In this study a multi-disciplinary approach has been adopted to resolve the taxonomy of the scleractinian coral *Montipora digitata*. The genus *Montipora* belongs to the family Acroporidae along with 3 other extant genera. *Montipora digitata* is a small branching coral often found in abundance on reef flats from the western Indian Ocean eastwards to Fiji. Within this species there are 2 morphs that

*To whom correspondence and reprint requests should be addressed. Carrer del Rosari 5, Secelles, Mallorca 07140, Spain. E-mail: benoir@maptel.es

for convenience shall be referred to as "yellow spatulate" (YS) and "fat finger" (FF) (Stobart et al. 1992, Stobart and Benzie 1994). Yellow-spatulate colonies tend to be green-yellow with some laterally compressed branch tips, whereas FF colonies are gray-brown and have rounded branch tips (Fig. 1). The 2 morphs are known to live sympatrically on inshore reef flats along the Great Barrier Reef, Australia, in Papua New Guinea, and in Sabah, Malaysia (pers. obs.). They are also likely to coexist at other locations where *M. digitata* is known to exist. Within specific locations, there is no evidence that the 2 morphs occupy different zones, and they are often found growing next to each other. Preliminary work suggested that the 2 morphs of *M. digitata* would not interbreed (Willis et al. 1992). They were later found to differ in the number and size of eggs they produce (Stobart et al. 1992); they were also confirmed not to interbreed (Stobart 1994) and to be genetically distinct (Stobart and Benzie 1994). These findings have led to the conclusion that the 2 morphs are different species. The aim of this study was to identify morphological features that could be used to consistently identify the 2 species and to examine museum specimens in order to name the species appropriately.

MATERIALS AND METHODS

Study sites

Colonies of both species used in this study were collected from reef flats at Magnetic Island and Orpheus Island off the North Queensland coast, Australia. Colonies at these locations were collected from Geoffrey Bay (n = 28) and Nelly Bay (n = 14) at Magnetic Island (19°10'S, 146°51'E), and Pioneer Bay (n = 11) at Orpheus Island (18°35'S, 146°29'E). Geoffrey Bay and Nelly Bay are separated by a small headland and are only 1 km apart. A further 2 samples each from Low Isles (Queensland) and Wewak (Papua New Guinea) were also included in the analyses (they were the only samples available from these 2 sites). As fragmentation of *Montipora digitata* is common, all colonies were collected from more than 5 m apart to reduce the chance of collecting clonemates. On collection, several branch tips were removed from each colony and stored in liquid nitrogen for identification using allozyme electrophoresis, the remaining colony was then placed in a weak sodium hypochlorite solution until all living tissue had been digested leaving a clean skeleton for taking measurements.

Electrophoretic identity

Referral to the FF and YS species throughout this paper is based on electrophoretic evidence, except in the case of colonies collected from Low Isles and Papua New Guinea for which there were no tissue specimens. Species identity was determined using the LT-2* fixed gene difference described in Stobart and Benzie (1994). The enzyme screened was peptidase EC 3.4.11* using leucyl tyrosine (LT) substrate with a LiOH buffer. Leucyl tyrosine formed 1 banded and 3 banded phenotypes corresponding to dimeric homozygotes and heterozygotes, respectively. The species were distinguished by a fixed gene difference at LT-2*, with all FF colonies having allele *100 and all YS colonies allele *55.

Morphometric study

Of the 28 colonies collected from Geoffrey Bay, thirteen were FF and 15 YS based on electrophoretic evidence. Of these, five FF and 5 YS colonies were collected that were "typical" morphological examples of the 2 species, the remainder were of uncertain morphology. Colonies collected from Pioneer Bay consisted of 6 FF and 5 YS, while at Nelly Bay there were 10 FF and 4 YS colonies based on electrophoretic evidence. Colonies from Nelly Bay were unusual in that both FF and YS colonies had spatulate branch tips. The FF and YS samples from Low Isles and Papua New Guinea represented "typical" morphological examples of the 2 species at the respective locations.

One of the most prominent features of members of the family Acroporidae is their lack of diagnostic skeletal features (Veron and Wallace 1984, Wallace and Willis 1994). The lack of features such as tuberculae and papillae, which are common in the

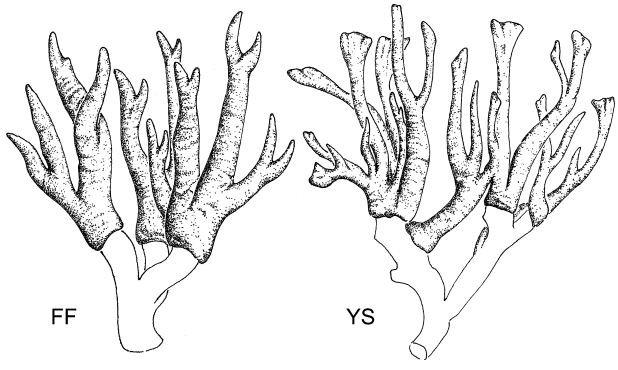

Fig. 1. Fat-finger (FF) and yellow-spatulate (YS) morphs of *Montipora digitata*.

genus *Montipora* but which do not occur in *M. digitata*, further reduces the amount of useful features for measurement. Features measured were branch tip width and breadth, corallite diameter, leading septal length, and inter-corallite distance (Fig. 2).

A feature that initially helps to distinguish the 2 species of *M. digitata* is the difference in branch tip morphology. Fat-finger colonies normally have rounded branch tips while yellow-spatulate colonies have explanate branch tips. The shape of branch tips was incorporated into the analysis by measuring the greatest branch tip width (W1), and W2, the breadth at 90° to W1 (Fig. 2). These measurements were made 0.5 cm from the branch tip. The ratio of W1 to W2 gives an estimate of the degree of branch tip flattening (i.e., of how spatulate they are). A total of 20 of each of the 2 branch tip measurements was made per colony from randomly selected branch tips.

Three corallite measurements were made using computer image analysis: corallite diameter (DI: the largest distance across a corallite), inter-corallite distance (IN: the distance between the center of corallites), and septa length (SE: the length of the leading septa). For each colony, five measurements of each variable were made from each of 4 branches chosen randomly. All measurements were obtained from corallites located 2-3 cm from the branch tip. This distance was considered far enough from the branch tip for corallites to be fully formed, yet not so close to the colony base that corallite morphology may have been affected by reduced light or increased sediment loads.

Standardization of the measurement of inter-corallite distance was achieved by selecting 5 corallites that formed a pentagon in the center of the "grabbed" frame and measuring the distance between each of them (Fig. 2). Both corallite diameter and septal length were measured from the 5 largest corallites in the frame. Selection of features in this manner is valid for comparison of the 2 species (as it is a standardized method for both of them), but it is not suitable for describing the variability of these features for taxonomic purposes. Consequently to account for the full extent of corallite variability in the 2 species, all corallites within the 4 sampled frames from 10 FF and 10 YS colonies were measured. Within each species the 2 most different colonies from each site (those furthest apart in the canonical discriminant analysis) were selected for measurement (except for samples from Papua New Guinea and Low Isles where only 1 sample was available per morph). Selecting the most different colonies provides a better estimate of the range of variation in corallite diameter and septal length for each of the 2 species. Septal shape was also compared between the 2 species. The shapes of the 1st cycle septa

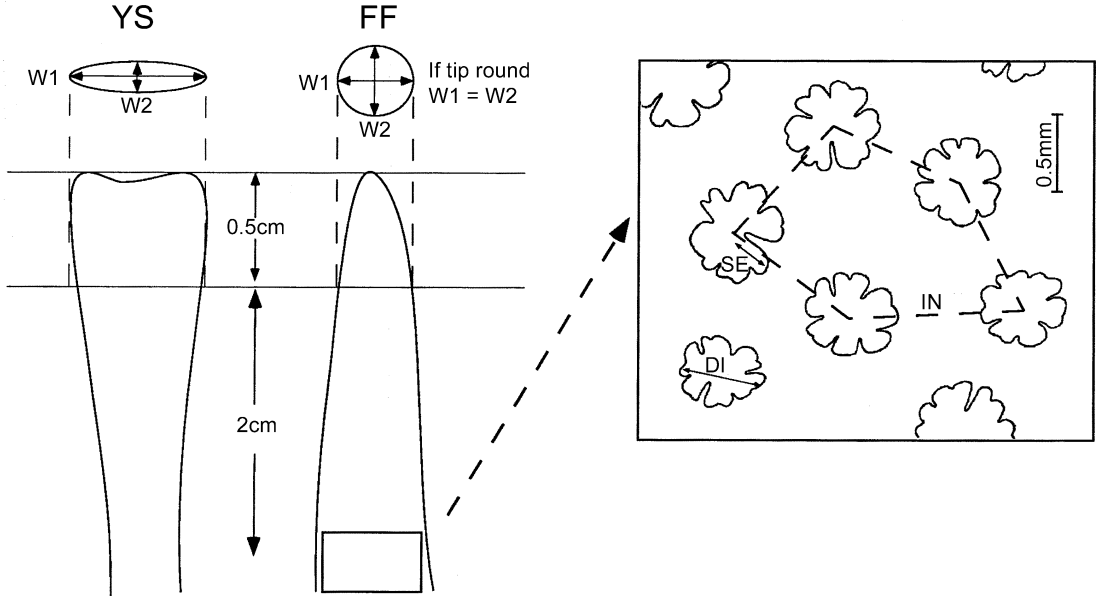

Fig. 2. Measurements made for morphometric analysis of FF and YS *Montipora digitata*. The greatest branch tip width (W1), and width at 90° to the greatest width (W2) were measured 0.5 cm from the branch tip. Corallite-level measurements are shown in the box. Inter-corallite distance, IN (- - -) was measured between the 5 corallites forming a pentagon nearest to the frame center; corallite diameter (DI) and leading septum length (SE) were measured from the 5 largest corallites in the video frame.

were classified as: 1) serrated: septa in the form of rows of spines; 2) lamino-serrated: individual septum occurring as a combination of spines and fused spines; and 3) laminar: septa consisting of continuous sheets of fused spines (see Fig. 3 for examples of serrated and laminar septa). Septa were examined from a total of 59 colonies (Geoffrey Bay: 14 FF and 14 YS; Nelly Bay: 14 FF and 6 YS; Pioneer Bay: 5 FF and 6 YS). For each colony the shape of all 1st cycle septa was recorded for 5 corallites from 3 randomly selected branches giving a total of 15 corallites examined per colony. In total, 509 FF corallites (septa n = 3059), and 374 YS corallites (septa n = 2247) were examined. Corallites were examined in the zone 2-3 cm from the branch tip used for the morphometric measurements described above.

Statistical analyses

Differences between individual morphological characters in FF and YS colonies were first compared using one-way analysis of variance. Alpha was adjusted to allow for multiple tests using the Bonferroni correction α/p, where p = number of tests (α = 0.0125). Data were tested for normality (using Cochran's test), and homogeneity of variances. Data were $\log_{10}$ transformed to meet the assumptions of the analysis of variance. Data for W1 did not meet the assumptions of ANOVA and were therefore analyzed using a non-parametric Kruskal-Wallis test (Chi-square approximation).

In order to look for the combined effects of skeletal characters, a nested multivariate analysis of variance (MANOVA, colony was nested within species) was performed using the variables diameter (DI), inter-corallite distance (IN), and branch-tip widths W1 and W2. Data were tested for multivariate normality using multivariate normality plots and multivariate Levene's test. In order to conform to multivariate normality, the data were $\log_{10}$ transformed. Septum length and branch-tip diameter (W1) were found to be correlated, so septum length was omitted from the multivariate analysis. The relationship between the species was visually investigated using canonical discriminant analysis (CDA). This technique finds the minimum number of dimensions that maximize the variation between a priori groups (in this case, colonies identified using allozyme electrophoresis). Confidence limits for group centroids in the canonical discriminant analyses were obtained using the formula (χ^2 2.05/n) (Seber 1984). All analyses were performed using SAS.

Validating septal shape as a distinguishing character

In order to determine the usefulness of septal shape for distinguishing the 2 species, an assessment of species identity was made using septal shape only. This was designed to rule out any possibility of bias in the description of shape caused by a priori knowledge of species status. Seventeen spatulate *Montipora digitata* branches were selected from Nelly Bay, where identification of fat-finger and yellow-spatulate *M. digitata* based on gross morphology is most difficult (as colonies that have spatulate branch tips are often FF based on allozyme electrophoresis results). The colonies were first identified using septal shape as the identification criterion, and

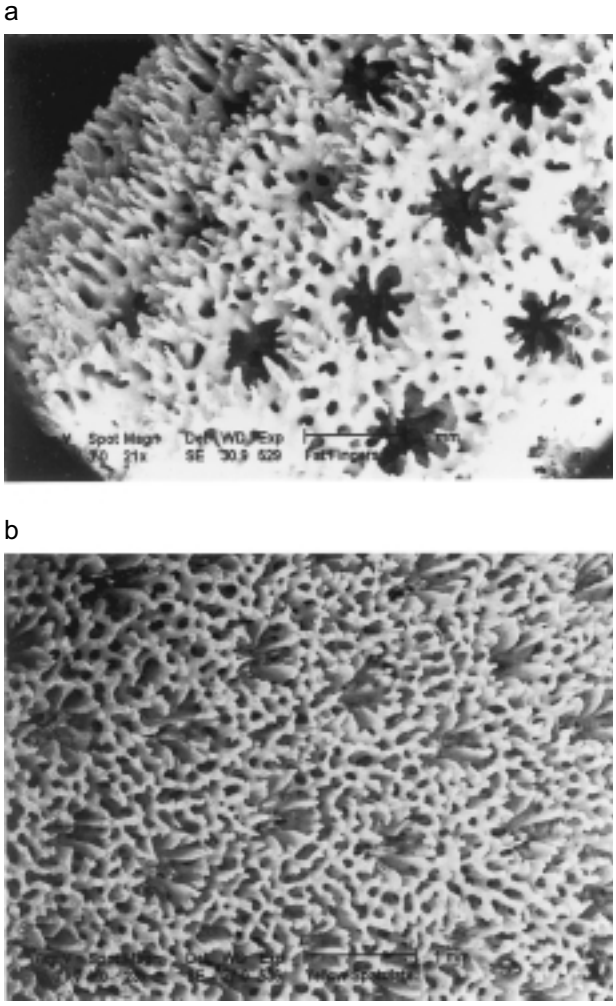

Fig. 3. Scanning electron micrographs of the skeletons of fat-finger (a) and yellow-spatulate (b) *Montipora digitata*. Fat-finger corallites contain serrated septa, while yellow-spatulate septa are laminar.

subsequently identification was confirmed using allozyme electrophoresis.

Examination of museum collections

Holotypes of 17 species of *Montipora* synonymous with *M. digitata* were examined to determine which pre-existing name would be appropriate to assign to either the YS or FF species of *M. digitata*. The shape of the septa was used to identify museum specimens. Other features such as the shape of branch tips were also noted, though the samples were often in poor condition (broken branch tips) and gross morphological features could not be evaluated. Colonies from original collections by the United States National Museum of Natural History (USNM), the British Museum of Natural History (BMNH), and the Australian Institute of Marine Science (AIMS) were examined. Corallite level measurements were made for colonies from the USNM (*M. tortuosa* Dana, 1846 no. 310 and *M. digitata* Dana, 1846 no. 312) using the same image analysis technique described above. These colonies were not included in the statistical analyses due to the lack of branch tips to measure.

RESULTS

Morphological differences

The 2 species of *M. digitata* previously identified using allozyme electrophoresis were found to differ morphologically. Analysis of variance indicates that corallite diameter, inter-corallite distance, and branch-tip diameter (W2) differ significantly between FF and YS colonies (Table 1). Branch-tip diameter (W1) also differed between species (χ^2 5.55, 1 df, $0.01 < p < 0.025$). There was no difference in leading septum lengths between the 2 species (Table 1). Despite the skeletal differences, no single character can be used to identify the species due to the large amount of overlap of the characters between them (Table 2).

The difference between the species was also apparent when the skeletal features were considered together. Multivariate analysis of variance testing for an overall species effect was significant (Pillai's trace = 0.27, F = 4.7, df = 52, $p < 0.01$). Canonical discriminant analysis showed that the 1st and 2nd canonical variables account for 62% and 22% of the variation between species, respectively. A plot of these 2 canonical variables shows that the 2 species tend to cluster on opposite sides of canonical axis 1 (Fig. 4). Corallite diameter and the smallest branch width were the most important factors governing the separation of the species, as determined from the bi-plots. A bi-plot is a representation of the relative contributions of each character (shown as arrow length), and the direction in which its influence moves the points on the plot (shown by the arrow's orientation). Both corallite diameter and the smallest branch width were larger for FF colonies. However, despite these differences there is an area of considerable overlap between colonies, and consequently combinations of measurements are not suitable for unambiguously distinguishing the 2 species.

Colonies from Nelly Bay were peculiar in that FF colonies tended to have spatulate branch tips, making species distinction from YS usng gross morphology very difficult. The unusual branch-tip morphology of Nelly Bay FF colonies was apparent in the CDA plot where some of the Nelly Bay FF colonies form a distinct cluster at the top left corner (Fig. 4). The difference in branch tip shape is readily apparent

Table 1. One-way analysis of variance comparing corallite measurements of *Montipora digitata* FF and YS colonies

Morphological feature	Variance source	Degrees of freedom	Sum of squares	Sum of squares	*F* Value	*P*
DI	species	1	0.890	0.890	15.159	***
	error	55	3.229	0.059		
IN	species	1	0.514	0.514	14.065	***
	error	55	2.010	0.037		
SEPTA	species	1	0.060	0.060	0.426	*
	error	55	7.700	0.140		
W2	species	1	0.905	0.905	9.912	**
	error	55	5.023	0.091		

DI: corallite diameter, IN: inter-corallite distance, SEPTA: leading septum length, and W2: greatest branch-tip width. Significance levels: *$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$.

when plots of branch-tip widths, W1 and W2, are compared between colonies from Geoffrey, Pioneer, and Nelly Bays (Fig. 5). Fat-finger colonies from Nelly Bay produced regressions with very poor slopes consistent with having a mixture of rounded and explanate branch tips similar to those of YS colonies (Fig. 5). Fat-finger colonies from Geoffrey Bay and Pioneer Bay had regressions with slopes closer to one consistent with having rounder branch tips.

Septal morphology

The shape of septa proved to be a distinguishing character between the 2 *Montipora* species. More than 90% of FF septa examined were serrated, whereas 60%-80% of yellow-spatulate septa examined were laminar (Fig. 6). The distribution of septal shapes was similar at all 3 bays examined. For FF colonies, no corallite examined had more than 1 laminar septum, with the exception of 2 corallites from Pioneer Bay colonies, one with 4, and another with 2. For YS colonies, the trend was not as clear; 35 corallites had less than 2 laminar septa per corallite and 8 had no laminar septa. However, the yellow-spatulate corallites deficient in laminar septa were not unique to 1 colony, and therefore laminar septa are always obvious in YS colonies providing several corallites are examined. The septal difference was also evident in FF and YS colonies from Low Isles and Papua New Guinea.

Though the numbers of septa in the 3 categories were recorded between 2 and 3 cm from the branch tip, qualitative observations suggest that the patterns of septal shape were similar throughout the colonies, including the branch tips. Of the 17 colonies from Nelly Bay initially identified using septal shape, only 6 were YS, and 11 were FF based on allozyme electrophoresis. The identifications based on septal morphology corresponded exactly to the allozyme electrophoresis results, indicating that septal shape provides a reliable way of separating the 2 species.

Comparison with museum specimens

Most of the museum specimens examined were identifiable either as FF or YS colonies based on

Table 2. Summary of morphometric measurements made for morphometric analysis (in mm) of FF and YS *Montipora digitata* colonies

		GB		NB		PB	
Var.	Statistic	FF	YS	FF	YS	FF	YS
	n	260	300	200	80	120	100
	mean	0.67	0.61	0.65	0.50	0.69	0.60
DI	range	(0.48-0.90)	(0.41-0.96)	(0.38-0.66)	(0.32-0.91)	(0.41-0.92)	(0.39-0.75)
	mean	1.18	1.10	1.16	0.98	1.28	1.13
IN	range	(0.69-1.71)	(0.67-1.55)	(0.75-1.72)	(0.61-1.47)	(0.85-2.22)	(0.80-1.52)
	mean	0.17	0.18	0.17	0.14	0.14	0.13
SE	range	(0.08-0.28)	(0.10-0.34)	(0.07-0.27)	(0.05-0.25)	(0.05-0.30)	(0.06-0.23)
	mean	0.64	0.66	0.80	0.67	0.54	0.60
WI	range	(0.40-1.29)	(0.34-1.90)	(0.30-2.20)	(0.33-1.20)	(0.39-0.94)	(0.32-1.43)
	mean	0.57	0.49	0.50	0.42	0.50	0.47
W2	range	(0.39-0.96)	(0.30-0.91)	(0.27-0.97)	(0.29-0.65)	(0.35-0.75)	(0.32-0.78)

		LI		PNG		Overall	
Var.	Statistic	FF	YS	FF	YS	FF	YS
	n	20	20	20	20	**620**	**520**
	mean	0.71	0.65	0.5	0.44	**0.66**	**0.59**
DI	range	(0.57-0.90)	(0.46-0.84)	(0.42-0.60)	(0.34-0.57)	**(0.38-0.92)**	**(0.32-0.96)**
	mean	1.34	1.17	1.12	0.89	**1.20**	**1.08**
IN	range	(1.02-1.81)	(0.80-1.58)	(0.88-1.38)	(0.56-1.23)	**(0.69-2.22)**	**(0.56-1.58)**
	mean	0.18	0.17	0.13	0.10	**0.16**	**0.16**
SE	range	(0.12-0.26)	(0.08-0.29)	(0.10-0.22)	(0.05-0.18)	**(0.05-0.30)**	**(0.05-0.34)**
	mean	0.85	0.81	0.59	0.62	**0.68**	**0.65**
W1	range	(0.65-1.12)	(0.49-1.20)	(0.40-0.81)	(0.36-1.03)	**(0.30-2.20)**	**(0.32-1.90)**
	mean	0.71	0.60	0.54	0.42	**0.54**	**0.47**
W2	range	(0.62-0.96)	(0.47-0.80)	(0.40-0.66)	(0.26-0.50)	**(0.27-0.97)**	**(0.26-0.91)**

Colonies were collected at: Geoffrey Bay (GB), Nelly Bay (NB), Pioneer Bay (PB), Low Isles (LI), and Papua New Guinea (PNG). Variables (Var.) measured were (DI): corallite diameter; (IN): inter-corallite distance; (SE): septa; (W1): greatest branch-tip width; (W2): branch-tip width at 90° to W1; *n*: number of measurements.

septal characteristics (Table 3). In accordance with the *International Code of Zoological Nomenclature* (Stoll et al. 1964), the names to be resurrected when synonymized species are found to be different should be those first assigned to them. Both species described here had also been collected by Dana in 1846, this being the earliest description of the species on record. Dana's holotype for *M. digitata* (Dana, 1846: USNM 312) clearly had laminar septa and therefore corresponds to a YS morphology, whereas the holotype for *M. tortuosa* (Dana, 1846: USNM 310) had serrated septa and therefore corresponds to an FF morphology.

Corallite characters for the USNM specimens were also measured using image analysis. The measurements are summarized in table 4, along with the measurements made for colonies collected during this study. Corallite diameter, inter-corallite distance, and leading septum length of USNM specimens were all larger for *M. tortuosa* (Table 4), further supporting the finding that this is an FF colony (however, the holotypes being from different sites with environmental differences could account for differences in the corallite characters measured). In view of the above, the 2 species can now be called *M. tortuosa* if they correspond to the FF description, and *M. digitata* if they correspond to the YS description. Representative specimens of these 2 species from this study have been lodged with the Museum of Tropical Queensland, Australia (*M. tortuosa* reg. Nos. G47814, G47816; *M. digitata* reg. no. G47815).

DISCUSSION

The 2 species of *Montipora digitata*, initially identified due to their reproductive incompatibility (Willis et al. 1992, Stobart 1994), and using allozyme electrophoresis (Stobart and Benzie 1994), can now also be distinguished morphologically. Although several differences were found between the species, only septal shape proved to be reliable for separating

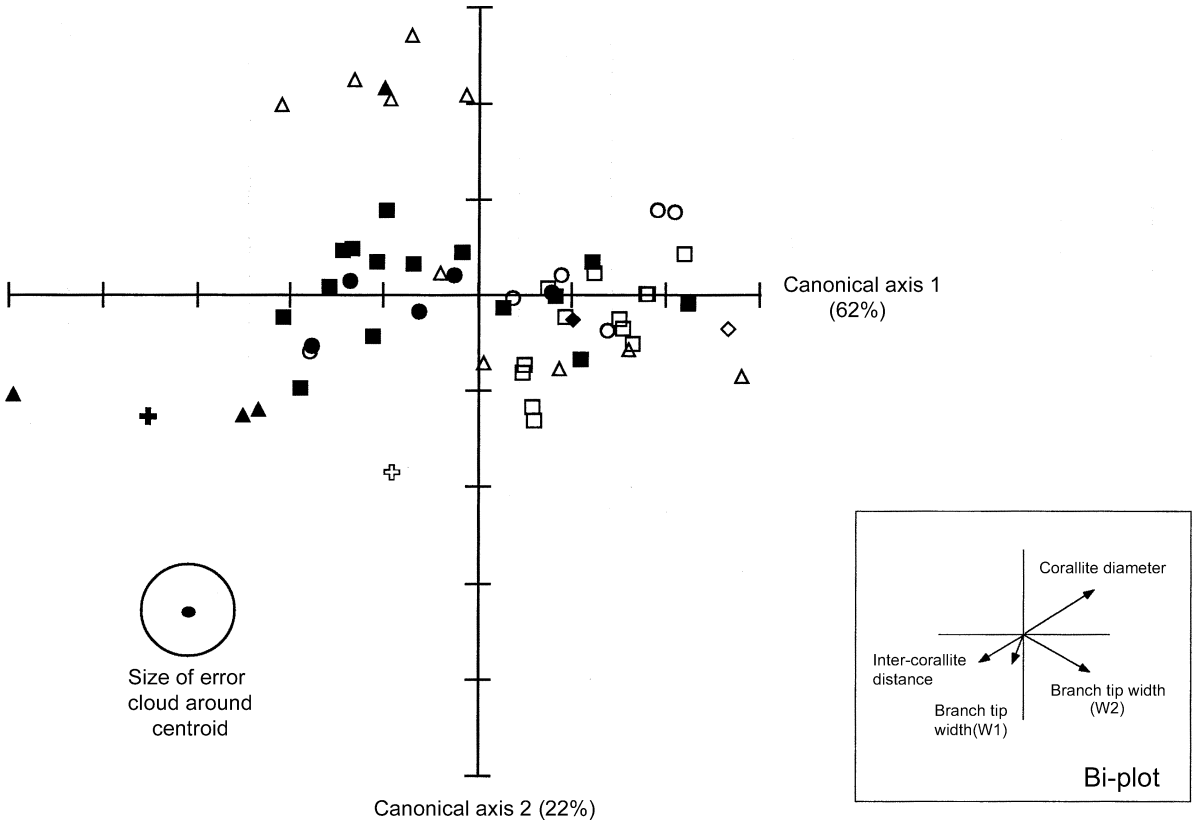

Fig. 4. Plot of canonical axes 1 and 2 for all FF (empty symbols) and YS (filled symbols) *Montipora digitata* colonies collected. Sites are represented by symbols: ■ Geoffrey Bay; ● Nelly Bay; ▲ Pioneer Bay; ◆ Low Isles; and ✚ Papua New Guinea. Symbols represent colony centroids, while the error cloud represents the 95% confidence interval around centroids. The bi-plot summarizes the total canonical structure. Each point is derived from 20 measurements per colony of the variables corallite diameter, inter-corallite distance, and branch widths W1 and W2.

them. The occurrence of laminar septa in FF colonies is so rare that lack of laminar septa alone can be used to distinguish this species. Dana's original collections of 1846 were reexamined using septal shape for identification. Dana had collected both FF and YS specimens and recognized them as *M. tortuosa* (FF) and *M. digitata* (YS), but they were later synonymised as *M. digitata* by Veron and Wallace (1984). Veron and Wallace (1984) did recognize 3 ecomorphs of *M. digitata*, but their morphological differences were based on how corallite size and spacing varied with depth, and did not distinguish between the FF and YS morphs. In view of the current evidence, *M. tortuosa* (Dana, 1846), and *M. digitata* (Dana, 1846) are the legitimate names for the FF and YS species, respectively, and they shall be referred to as such from here onwards.

The septal difference between the 2 species was evident in colonies from all sites, including those collected 1500 km away in Papua New Guinea. Septal shape was also a reliable species indicator for colonies of unusual morphology from Nelly Bay, and is therefore a diagnostic character that appears to be stable over a wide geographic area and throughout a range of habitats. Septa play a key role in the support and separation of the mesenteries, and they are the first skeletal structures apparent after the deposi-

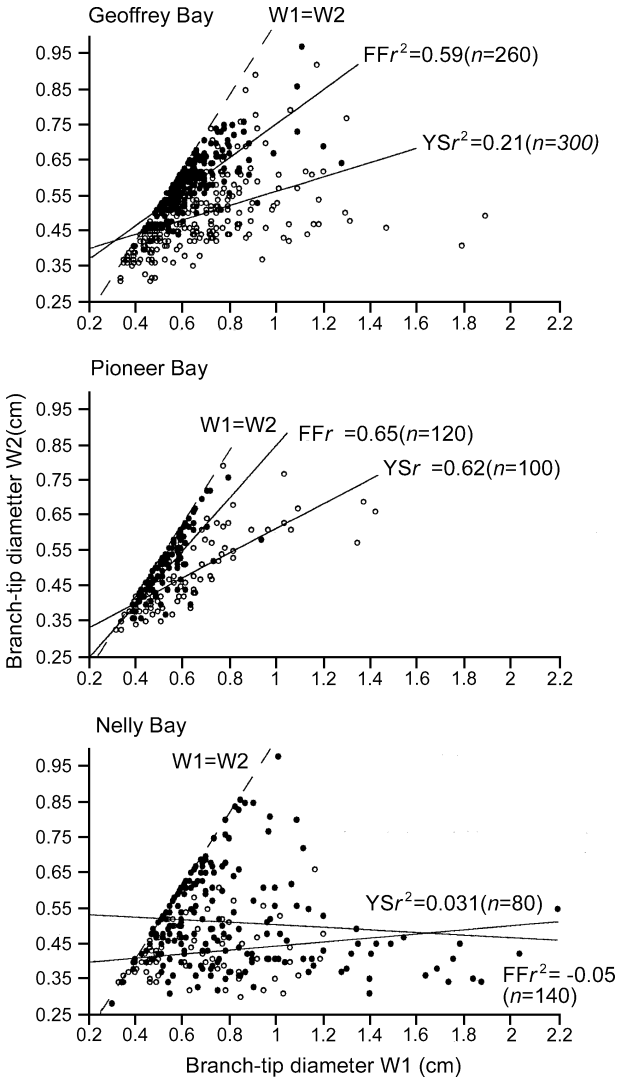

Fig 5. Scattter plots showing the relationship between greatest branch-tip diameter (W1), and diameter at 90° to the greatest branch-tip diameter (W2), for FF (●) and YS (○) colonies of *Montipora digitata* at Geoffrey Bay, Pioneer Bay, and Nelly Bay. Regression lines of best fit for FF and YS colonies are plotted as solid lines; dashed lines represent round branch-tips (i.e., W1 = W2 equivalent to regression slope of 1). *n*: number of branch tips.

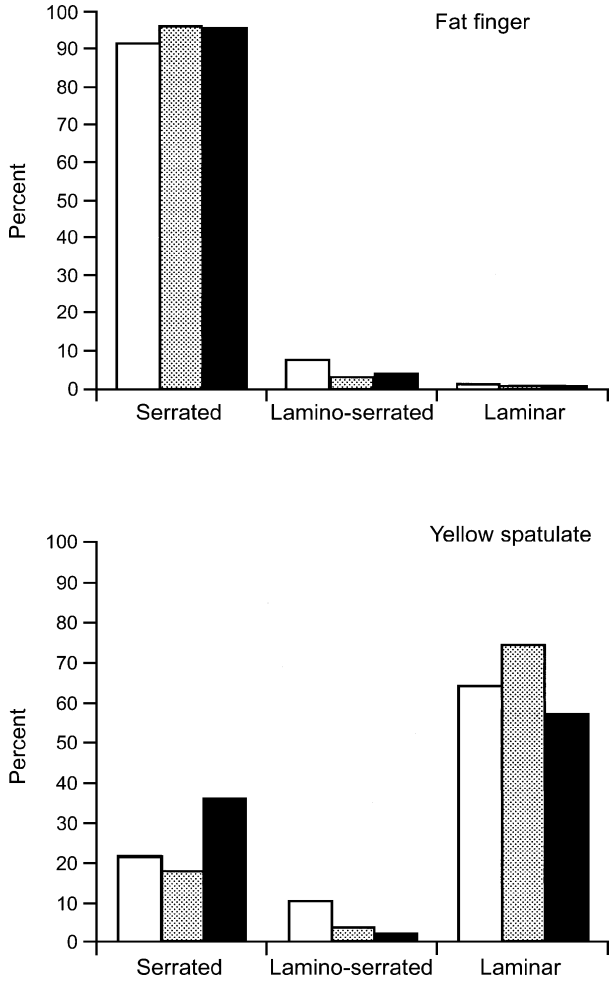

Fig. 6. Percentage of serrated, lamino-serrated and laminar septa in FF and YS colonies of *Montipora digitata* from Geoffrey Bay (□), Nelly Bay (▨), and Pioneer Bay (■). Number of septa counted: Geoffrey Bay FF = 1259, YS = 1259; Nelly Bay FF = 1260, YS = 540; Pioneer Bay FF = 540, YS = 448.

tion of the skeletal plate (Wells 1956). Septa are also important taxonomic features, with their shape, size, and number all being used to describe species to varying degrees (e.g., Veron and Wallace 1984, Veron, 1986). Although septa are commonly used to identify species of *Montipora*, it is rare for a single feature to be so different between species as there is a general lack of good diagnostic features for species within the genus *Montipora* (Veron and Wallace 1984), and most other coral genera (e.g., *Porites*, Brakel 1977; *Platygyra*, Miller 1994). Also septa within the genus *Montipora* are seldom lamellate (Bernard 1897, Nemenzo 1967), and skeletal characters are not generally very stable over wide geographic areas in scleractinian corals (Veron 1995).

Other skeletal characters compared between the species did not prove species specific as they overlapped considerably. This finding is to be expected as overlap in morphological characters between coral species is generally very common (Brakel 1977, Foster 1982). For example, overlap in morphological characters has been found in morphometric studies of *M. annularis* (Van-Veghel and Bak 1993), *Porites* (Brakel 1977), and *Platygyra* (Miller 1994). Within the genus *Porites*, species have been found to be so similar that Brakel (1977) referred to inter-specific variation as being almost continuous. As a result, Garthwaite et al. (1994) have suggested that poritid taxonomy is unlikely to be resolved using morphological data alone. In the case of this study, morphological data does show an overall difference between the 2 species in spite of the overlap of characters. *Montipora tortuosa* colonies generally have larger corallites that are further apart from each other than those of *M. digitata* colonies. Corallite diameter has also been found to differ between members of the genera *Platygyra* (Miller 1994) and *Flavellum* (Cairns 1989). Similarly, inter-corallite distance proved useful for the study of *Montastraea annularis* morphotypes (Van-Veghel and Bak 1993). *Montipora tortuosa* and *M. digitata* can normally be distinguished in the field using their color and branch-tip morphology alone; *M. tortuosa* has rounded branch tips and *M. digitata* is normally yellow-green. It is this difference that probably led Dana to conclude that they were different species. However in some cases, there will be an element of uncertainty as both of these features can vary considerably. It is likely that this variability prompted Veron and Wallace (1984) to group the 2 species. Variability in branch-tip morphology and color was particularly evident in colonies from Nelly Bay in which *M. digitata* colonies were not always yellow-green, and *M. tortuosa* colonies had many spatulate branch tips. This suggests that there may be an environmental effect in Nelly Bay. Nelly Bay is different

Table 3. Species synonymous with *Montipora digitata* and their classification as FF or YS morphs

Species name	Collection site	Authorship	Located in	Species
M. spatula (SH)	Warrior Is. GBR	Bernard 1892	BMNH	FF
M. palmata	Fiji	(Dana) Bernard (1896)	AIMS	?
M. tortuosa (H)	Singapore	Dana 1846	USNM 310	FF
M. poritiformis (H)		Verrill 1869	AIMS	YS
M. ramosa (H)	Gulf of Mananar	Bernard 1888	BMNH	FF
M. compressa			AIMS	FF
M. indentata (H)		Bernard 1897	AIMS	FF
M. fruticosa	GBR	Bernard 1897	BMNH	YS
M. fruticosa		Bernard 1897	AIMS	FF?
M. digitata (H)	Fiji	Dana 1846	USNM 312	YS
M. digitata (Sp. 365)	Hope Island	Dana 1846	AIMS, Fig 196 in S.E.A.	YS
M. digitata (Sp. 365)	Broadhurst Reef	Dana 1846	AIMS, Fig 195 in S.E.A.	FF
M. digitata (Sp. 365)	Berwick Is.	Dana 1846	AIMS, Fig 194 in S.E.A.	YS
M. irregularis (H)	Zamboanga	Quelch 1886	BMNH	FF
M. marenzerelli		Bernard 1897		YS
M. gaimardi (SY)	Solomon Is. Australia Tongatabu	Bernard 1897	BMNH	YS
M. laris (SH)	Banda	Quelch 1886	BMNH	YS
M. spongilla (H)	Christmas Is.	Bernard 1897	BMNH	YS
M. spicata (H)		Bernard 1897	BMNH	YS
M. fossae (SY)		Crossland 1952	BMNH	YS?
M. nana (H)	Port Molle	Bernard 1882	BMNH	FF?

For species H: holotype, SH: schizo-holotype, and SY: syntype. For location of colonies AIMS = Australian Institute of Marine Science, BMNH = British Museum of Natural History, and USNM = United States National Museum. S.E.A. is *Scleractinia of Eastern Australia* Vol. V.

from the other sites as colonies are only rarely exposed at low tide, and they are more exposed to wave action than at the other 2 sites. Interestingly the spatulate branch tips of *M. tortuosa* colonies in Nelly Bay are oriented parallel to the shoreline offering maximum resistance to wave action. This trend is not evident in *M. digitata* colonies whose spatulas tend not to be parallel to the shore. The positioning of spatulas parallel to the shore is counter-intuitive and would make an interesting subject for further investigation. Had Dana collected his samples from this area, he would possibly have concluded that he was dealing with a single species.

The species boundaries between *M. tortuosa* and *M. digitata* are very clear. The 2 species represent good "biological species" as they are reproductively isolated, and there is evidence that there is a strong barrier to fertilization prior to egg activation (Stobart 1994). At the same time, the species are morphologically distinct, and therefore good examples of "morphological species". This lends support to the notion that the biological species concept can be applied to some corals that have traditionally been distinguished by their morphology. However, one cannot generalize as reproductive and morphological data are not always in agreement (Miller 1994, Miller and Babcock 1997, Szmant et al. 1997 but also see Knowlton et al. 1997), and hybridization appears to be common in many coral species (Miller 1994, Wallace and Willis 1994, Miller and Babcock 1997, Miller and Benzie 1997, Szmant et al. 1997). In view of this, one cannot assume that the biological species concept will apply to all coral groups.

In summary, the identification of a species-specific morphological character has made it possible to rename the FF and YS morphs of *M. digitata* as *M. tortuosa* and *M. digitata*, respectively. Furthermore, the analysis of other skeletal characters by univariate

Table 4. Summary of morphometric measurements (mm) for *Montipora tortuosa* (FF) and *M. digitata* (YS) colonies collected from all sites during this study, and for holotypes collected by Dana 1846 (USNM codes 310 = *M. tortuosa* and 312 = *M. digitata*)

Variable	Statistic	Species			
		M. tortuosa FF	*M. tortuosa* holotype (USNM 310)	*M. digitata* YS (USNM 312)	*M. digitata* holotype
DIAM	*n*	10 (299)	1 (15)	10 (311)	1 (39)
	mean	0.600	0.531	0.542	0.463
	stdev	0.127	0.043	0.134	0.071
	min	0.190	0.430	0.260	0.320
	max	0.907	0.590	0.963	0.590
SEPTA	*n*	10 (272)	1 (15)	10 (266)	1 (21)
	mean	0.162	0.131	0.145	0.114
	stdev	0.044	0.031	0.051	0.021
	min	0.055	0.080	0.050	0.080
	max	0.302	0.190	0.336	0.150
INTCOR	*n*	31 (620)	1 (15)	26 (520)	1 (20)
	mean	1.197	1.341	1.084	1.076
	stdev	0.211	0.174	0.180	0.157
	min	0.689	1.040	0.559	0.790
	max	2.218	1.770	1.580	1.410
W1	*n*	31 (620)		26 (520)	
	mean	0.677		0.653	
	stdev	0.234		0.224	
	min	0.300		0.320	
	max	2.200		1.900	
W2	*n*	31 (620)		26 (520)	
	mean	0.540		0.474	
	stdev	0.109		0.100	
	min	0.270		0.260	
	max	0.970		0.910	

DIAM: maximum corallite diameter, SEPTA: leading septum lenth, INTCOR: inter-corallite distance, W1: greatest branch tip width, W2: smallest branch tip width, *n*: number of colonies sampled and total number of measurements taken (in brackets).

and multivariate analysis shows further differences between the species, although no other skeletal characters are diagnostic. It is significant that the more traditional method of searching a colony visually for differences has led to the discovery of a character that can differentiate the 2 species. However, without a priori species identification using allozyme electrophoresis, septal shape would probably not have been identified as a "diagnostic" character. Neither would an exclusively morphometric study have identified the species, due to the considerable amount of overlap of skeletal characters. This study therefore highlights the value of a multiple-technique approach to coral taxonomy, each alternative method used acting as a test for the other and therefore reducing the chance of an erroneous conclusion.

Acknowledgments: I thank Keith Martin-Smith, Allen Chen, Bill Burnett, Sarah Stobart, Craig Mundy, Bette Willis, Carden Wallace, Jackie Wolstenholme, and Molly Cummings for their assistance in the field. Natalie Moltschaniwskyj, Mark McCormick, Bette Willis, and Karen Miller kindly made useful comments on the manuscript. I also thank the Australian Institute of Marine Science, the British Museum of Natural History, and the United States National Museum of Natural History for access to coral collections. This study was funded by a CFSP scholarship, a GBRMPA augmentative grant, and an ARC grant to B. Willis/K. Miller/B. Stobart.

REFERENCES

Ayre DJ, JEN Veron, SL Dufty. 1991. The corals *Acropora palifera* and *Acropora cuneata* are genetically and ecologically distinct. Coral Reefs **10:** 13-18.

Ayre DJ, BL Willis. 1988. Population structure in the coral *Pavona cactus*: clonal genotypes show little phenotypic plasticity. Mar. Biol. **99:** 495-505.

Bernard HM. 1897. Catalogue of the Madreporarian corals in the British Museum (natural history). Br. Mus., 3.

Brakel WH. 1977. Corallite variation in *Porites* and the species problem in corals. Proc. 3rd Intl. Coral Reef Symp., Miami, 2-5 June 1977. **1:** 458-462.

Cairns CD. 1989. Discriminant analysis of Indo-West Pacific *Flabellum*. Mem. Assoc. Australas. Palaeontols. **8:** 61-68.

Eldredge N. 1993. What, if anything, is a species? *In* WH Kimbel, LB Martin, eds. Species, species concepts, and primate evolution. New York: Plenum Press. pp. 3-20.

Foster AB. 1982. Species overlap in reef-corals and its evolutionary significance. Abstracts, Geol. Soc. Am. **14:** 491.

Garthwaite RL, DC Potts, JEN Veron, TJ Done. 1994. Electrophoretic identification of poritid species (Anthozoa: Scleractinia). Coral Reefs **13:** 49-56.

Knowlton N, JL Mate, HM Guzmán, R Rowan, J Jara. 1997. Direct evidence for reproductive isolation among the three species of the *Montastraea annularis* complex in Central America (Panama and Honduras). Mar. Biol. **127:** 705-711.

Knowlton N, E Weil, LA Weight, HM Guzmán. 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. Science **255:** 330-333.

Lang JC. 1984. Whatever works: the variable importance of skeletal and of non-skeletal characters in scleractinian taxonomy. Palaeontogr. Am. **54:** 18-44.

Lopez JV, R Kersanach, SA Reiner, N Knowlton. 1999. Molecular determination of species boundaries in corals: genetic analysis of the *Montastraea annularis* complex using amplified fragment length polymorphisms and microsatellite marker. Biol. Bull. **196:** 80-93.

Lopez JV, N Knowlton. 1997. Discrimination of species in the *Montastraea anularis* complex using multiple genetic loci. Proc 8th Intl. Coral Reef Symp., Panama, June 24-29. **2:** 1613-1618.

Miller KJ. 1994. Morphological variation in the coral genus *Platygyra*: environmental influences and taxonomic implications. Mar. Ecol. Prog. Ser. **110:** 19-28.

Miller KJ, RC Babcock. 1997. Conflicting morphological and reproductive species boundaries in the coral genus *Platygyra*. Biol. Bull. **192:** 98-110.

Miller KJ, JAH Benzie. 1997. No clear genetic distinction between morphological species within the coral genus *Platygyra*. Bull. Mar. Sci. **61:** 907-917.

Nemenzo F. 1967. Systematic studies on Philippine shallow-water scleractinians: VI. Suborder Astrocoeniida (*Montipora* and *Acropora*). Nat. Appl. Sci. Bull. Univ. Phillipines **20:** 1-141.

Seber GAF. 1984. Multivariate observations. New York: J Wiley, 686 pp.

Stobart B. 1994. Delimiting coral species using alternative techniques: *Montipora digitata* (Dana, 1846), a case study. PhD dissertation, James Cook Univ. of North Queensland.

Stobart B, RC Babcock, BL Willis. 1992. Biannual spawning of three species of scleractinian coral from the Great Barrier Reef. Proc. 7th Intl. Coral Reef Symp., Guam. pp. 494-499.

Stobart B, JAH Benzie. 1994. Allozyme electrophoresis demonstrates that the scleractinian coral *Montipora digitata* is two species. Mar. Biol. **118:** 183-190.

Stoll NR, RP Dollfus, J Forest, ND Riley, CW Sabrosky, CW Wright, RV Melville. 1964. International code of zoological nomenclature adopted by the XV Congress of Zoology. London: International Trust for Zoological Nomenclature.

Szmant AM, E Weil, MW Miller, DE Colón. 1997. Hybridization within the species complex of the scleractinian coral *Montastraea annularis*. Mar. Biol. **129:** 561-572.

Van-Veghel MLJ, RPM Bak. 1993. Intraspecific variation of a dominant Caribbean reef building coral, *Montastrea annularis*: genetic, behavioral and morphometric aspects. Mar. Ecol. Prog. Ser. **92:** 255-265.

Veron JEN. 1986. Corals of Australia and the Indo-Pacific. London: Angus Robertson.

Veron JEN. 1995. Corals in space and time: biogeography and evolution of the scleractinia. London: Comstock Cornell.

Veron JEN, CC Wallace. 1984. Scleractinia of eastern Australia. Part V. Family Acroporidae. Monogr. Ser. Aust. Inst. Mar. Sci. Vol. 6. 422 pp.

Wallace CC, BL Willis. 1994. The systematics of *Acropora*: the effect of new biological findings on species concepts. Ann. Rev. Ecol. Syst. **25:** 237-262.

Wells JW. 1956. Scleractinia. *In* RC Moore, ed. Treatise on invertebrate paleontology. Coelenterata. Univ. Kansas Press. pp. 328-371.

Willis BL. 1990. Species concepts in extant scleractinian corals: considerations based on reproductive biology and genotypic population structures. Syst. Bot. **15:** 136-149.
Willis BL, DJ Ayre. 1985. Asexual reproduction and genetic determination of growth form in the coral *Pavona cactus*: biochemical, genetic and immunogenic evidence. Oecologia **65:** 516-525.
Willis BL, RC Babcock, PL Harrison, CC Wallace. 1992. Experimental evidence of hybridisation in reef corals involved in mass spawning events. Abstract 7th Intl. Coral Reef Symp., Guam. p. 109.

利用遺傳與形態測量的證據重新評估指表孔珊瑚的分類

Ben Stobart[1]

近來有關生殖的研究證明兩型的指表孔珊瑚應為兩個不同的種。本研究檢驗珊瑚分類所用的骨骼形態特徵，並進一步為這兩個種正名。以單變量與多變量的方法分析五個骨骼特徵，顯示二者在形態上的確具有差別。但是數據分析時的重疊性使得這兩種分析方法並不適用於物種的鑑定。進一步分析隔片則發現其形狀具有種別性。以隔片的形狀檢驗博物館的模式標本，顯示這兩個物種分別為指表孔珊瑚與扭表孔珊瑚。本研究強調以多種技術從事珊瑚分類的可行性，而且不同技術之間可作交叉檢驗，以減少錯誤結論的產生。

關鍵詞：珊瑚，表孔珊瑚，分類，形態測量學。

[1]Department of Marine Biology, James Cook University of North Queensland, Townsville, QLD 4811, Australia