

Fig. 4.3. Calical surfaces and transverse thin sections of the three species. SEM photos of A, *Montastraea annularis* (NK465); B, *M. franksi* (NK95-3); C, *M. faveolata* (NK428). Thin sections of D, *M. annularis* (NK464); E, *M. franksi* (NK426); F, *M. faveolata* (NK490). Septa of *M. annularis* and *M. franksi* slope gently from the wall to the columella, and their corallite walls are formed by coalescing septa and costae ("septothecal"). The septa and wall are thinner and more regular in *M. annularis* than in *M. franksi*. In contrast, septa of *M. faveolata* are noticeably more elevated and drop steeply from the wall to the columella. The corallite walls of *M. faveolata* are formed by dissepiments ("parathecal"). Scale bar = 1 mm.

appear more closely related to one another than to *M. franksi*. Thus, the new thin-section characters are effective at distinguishing species in fossil material, but perhaps less so at revealing their fine-scale evolutionary relationships.

Landmark analyses will never reveal evolutionary relationships accurately, however, if the landmarks are nonhomologous. Recent analyses of wall structure in the *M. annularis* complex (fig. 4.3D–F) suggest that there are important differences in the components making up the wall between *M. faveolata* and the other two taxa. In *M. faveolata*, the septa usually do not thicken significantly, and the wall is formed primarily by dissepiments. In contrast, in *M. franksi*, the wall is usually formed by septal thickening, and thick costae extend variably between adjacent corallites. In *M. annularis*, the wall structure is similar to *M. franksi*, except the costae are less variable and not as well developed. These observations are preliminary (data from appropriate outgroups are lacking), but they suggest that evolutionary relationships assessed from thin-section characters may match the results of molecular and three-dimensional morphological analyses once the landmarks are homologous.

The Fossil Record of Caribbean *Montastraea*

Comparably detailed analyses have not yet been applied to fossil material. However, cluster and canonical discriminant analysis of linear measurements and septal counts for Miocene to Pleistocene *Montastraea* (Budd 1990; Budd 1991; Budd et al. 1992; Budd, Johnson, and Potts 1994; Budd and Johnson 1997) reveal at least 16 apparent species of *Montastraea* from Caribbean localities over the past 50 million years. Preliminary phylogenetic reconstructions suggest that the genus consists of two distinct evolutionary clades that diverged during Eocene time. Clade I contains at least ten species with <36 septa per corallite, and clade II at least six species with >36 septa per corallite (Budd 1991; <http://porites.geology.uiowa.edu>). The former includes the *M. annularis* complex (~5.6–0 Ma) and the *M. limbata* complex (16.2–1.5 Ma), and the latter includes the *M. cavernosa* complex (8.3–0 Ma) (fig. 4.4).

The oldest occurrences of the *M. annularis* complex are of *M. faveolata* and *M. franksi* in the Seroe Domi Formation of Curaçao in horizons whose age dates range from 5.6 to 3 Ma. The next oldest occurrences of the complex are for these two species in the Pinecrest Sandstone of Florida (3.5–3 Ma) and the Buenos Aires reef trend of the Limón Group of Costa Rica (3.2–2.9 Ma). The oldest occurrences of the third species in the complex, *M. annularis*, are also in the Seroe Domi Formation but are higher in the section and have age dates of 2.6–2 Ma. The next oldest occurrences of *M. annularis* are in the Bahamas Drilling Project cores at

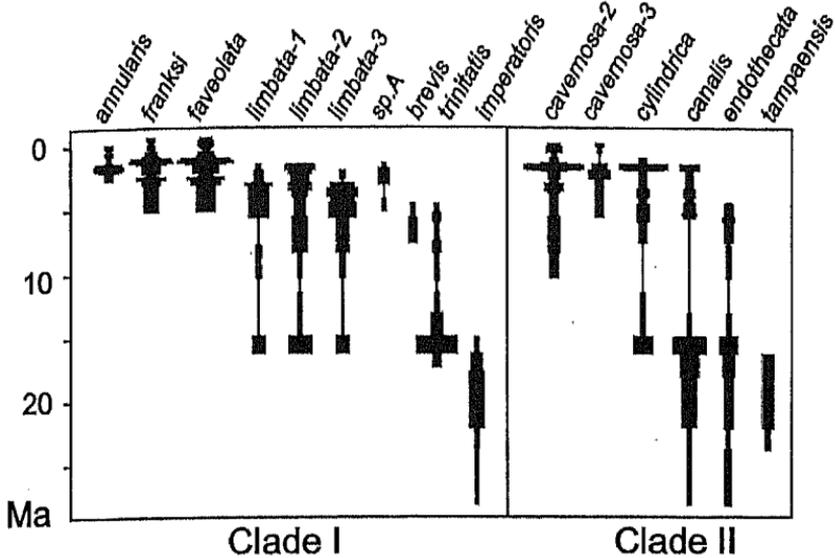


Fig. 4.4. Spindle diagram showing the stratigraphic ranges of the 16 species of *Montastraea* known from the late Oligocene to Recent. The width of each line is proportional to the number of localities (total = 112) in which the species occurred. Occurrence data are based on Budd and Johnson 1997 and Budd 1991. The *M. annularis* complex arose at the onset of turnover between 5.6 and 3 Ma and overlapped with the *M. limbata* complex.

intervals with age dates of 1.8–1.6 Ma. These data suggest that *M. faveolata* and *M. franksi* arose early during the evolution of the complex, whereas *M. annularis* appeared a million or more years later (fig. 4.4). This temporal pattern of divergence agrees with the genetic results above, and indicates that the distinctiveness of these morphologies has been maintained for millions of years. Furthermore, in Curaçao, the three taxa can be recognized (together with an additional, now extinct form) from 125,000-year-old terraces. Their local distribution patterns broadly resemble those found today (Pandolfi, Jackson, and Geister, this volume; Pandolfi and Jackson 2001), suggesting long-term constancy of ecological roles as well.

Conclusions

As the previous summary indicates, many years have been devoted to resolving the species controversy in the *M. annularis* complex. In the southern Caribbean (i.e., Panama and Curaçao) evidence for the three taxa is relatively strong, although we still have no unambiguous genetic tools for distinguishing *M. annularis* and *M. franksi*. In the northern Caribbean, numerous forms that are difficult to place make the picture less

clear-cut: are they hybrids or unique taxa that do not occur farther south? The persistence of such uncertainties is unsettling, considering the effort that has been invested in trying to resolve the nature of these taxa and their ecological importance.

Species boundaries in many other Caribbean taxa are even less clear, in part because they are largely unstudied. Table 4.1 summarizes various species and forms whose status is debatable. Taxonomic controversies swirl around many of the dominant reef-building genera of the Caribbean, but in the absence of a "solution" to the *Montastraea* problem, it is no wonder that scientists and funding agencies are reluctant to become involved. Many of the forms listed in table 4.1 may turn out to be good, conventional species, and Veron (1995) himself argued that the limited geographic scale of the Caribbean would be less likely to promote evolutionary reticulation and its attendant problems for species recognition.

In the Pacific, Veron's idea (1995) that species are rather arbitrary units due to widespread hybridization has changed the focus of discussion and research, and mismatches between morphological, reproductive, and genetic species are often interpreted in light of his hypothesis (e.g., Willis

Table 4.1. Modern Caribbean reef coral species whose taxonomic status is uncertain

Species	Reference
<i>Stephanocoenia intersepta</i> (2 morphs)	Goreau and Wells 1967; Foster 1987
<i>Acropora prolifera</i>	Vaughan 1901; Knowlton, pers. observation
" <i>Agaricia</i> " <i>agaricitis</i> (>3 morphs), "A." <i>crassa</i>	Wells and Lang 1973; Van Moorsel 1983; Stemann 1991; Morse 1993
<i>Agaricia fragilis</i> (2 morphs)	Wells and Lang 1973
<i>Siderastrea siderea</i> (2 morphs)	Budd and Guzman 1994; Knowlton and Budd, pers. observation
<i>Porites astreoides</i> (2 morphs)	Weil 1993; Potts et al. 1993; Budd, Johnson, and Potts 1994
<i>Porites furcata</i> , <i>P. porites</i>	Potts et al. 1993; Budd, Johnson, and Potts 1994
<i>Porites divaricata</i> (2 morphs)	Potts et al. 1993; Budd, Johnson, and Potts 1994
<i>Diploria labyrinthiformis</i> (2 morphs)	Matthai 1928; Johnson, pers. observation
<i>Manicina areolata</i> (>3 morphs), <i>M.</i> <i>mayori</i>	Wells 1936; Johnson 1991
<i>Colpophyllia natans</i> (2 morphs), <i>C.</i> <i>amaranthus</i>	Matthai 1928; Budd and Johnson 1999
<i>Montastraea cavernosa</i> (>2 morphs)	Lasker 1981; Budd 1993
<i>Meandrina meandrites</i> (2 morphs)	Goreau and Wells 1967
<i>Dichocoenia stokesi</i> (2 morphs)	Matthai 1928; Wells 1973
<i>Eusmilia fastigiata</i> (2 morphs)	Wells 1973

Notes: Some species have fuzzy species boundaries; others may consist of species complexes. Species of *Mycetophyllia* are also debated (Wells 1973).

et al. 1997; Odorico and Miller 1997; Hatta et al. 1999). Because of the enormous diversity that researchers on Pacific corals must confront, however, genetic studies remain preliminary, morphological homologies have not been scrutinized in detail, morphometric analyses such as those pioneered by Cheetham are generally lacking, and species from fossil deposits have not been carefully analyzed using modern morphological techniques. It thus remains unclear whether coral species in the Pacific are fundamentally different in character from their Caribbean counterparts.

Resolving species boundaries in corals is an important task for marine ecology (see discussion in Knowlton 1993; Knowlton and Jackson 1994), evolutionary biology, and paleontology (Budd and Coates 1992). Poorly defined species compromise phylogenetic analyses (Jackson and Cheetham 1994), estimation of rates of molecular evolution depends on recognizing species in fossil deposits, and management of coral reefs requires knowing which taxa are capable of interbreeding. Answering evolutionary questions of fundamental importance, such as whether most morphological change is associated with speciation ("punctuated equilibrium") and whether morphological changes during speciation are random or caused by selection (Cheetham et al. 1993, 1994; Cheetham and Jackson 1995), requires that we be able to show whether morphological and genetic divergence are concordant in living forms (Jackson and Cheetham 1990).

Throughout the tropics, solution of the coral species problem will require a multifaceted approach, drawing on insights from observations on living colonies, combined with genetic analyses and sophisticated morphological studies of the type pioneered and used with such success by Alan Cheetham. Our ongoing studies of *Montastraea* suggest that species boundaries may be difficult to detect both morphologically and genetically, requiring that we split to the highest level of statistical significance in morphological analyses and search widely for diagnostic genetic markers. In this light, negative evidence for differentiation (e.g., Medina et al. 1999) may be a particularly unreliable guide for making decisions about species boundaries in corals.

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