A NEW, EXTINCT PLEISTOCENE REEF CORAL FROM THE *MONTASTRAEA* "*ANNULARIS*" SPECIES COMPLEX

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ABSTRACT—A new species of the *Montastraea* "*annularis*" species complex is herein described from Pleistocene coral reefs of the Caribbean Sea. The species, *Montastraea nancyi* n. sp., had a broad geographic distribution at mainly insular sites 125 Ka. It has a fossil record extending from >600 Ka (thousand years) to 82 Ka, both first and last occurrences exclusively on the island of Barbados. It also had a broad environmental tolerance, occurring in fringing, windward back-reef and reef-crest, leeward reef-crest, and lagoonal patch-reef environments. In every habitat in which it lived, there are examples that it either dominated the coral fauna or shared dominance with *Acropora palmata*, a dominant shallow water coral in high-energy Pleistocene and modern reefs. The extinction of *Montastraea nancyi* resulted in evolutionary and ecological change in surviving members of the *M.* "*annularis*" species complex.

INTRODUCTION

MONTASTRAEA "*ANNULARIS*" (Ellis and Solander, 1786) is one of the most dominant corals of living (Goreau, 1959) and ancient (Geister, 1980) Caribbean reefs. Because of its seemingly limitless ability for phenotypic plasticity in growth form (Graus and Macintyre, 1982), and a distribution ranging from the intertidal to over 80 m water depth (Goreau and Wells, 1967), this coral was long considered the archetypal generalist (Connell, 1978). The extensive variability in colony morphology (columns, massive heads, and plates) exhibited over this range in water depth was believed to be an adaptive response to differing light levels (Graus and Macintyre, 1976). But in the last 10–15 years, a number of features have been found to covary with the different types of colony morphologies, including allozymes, reproductive biology, aggressive behavior, ecology, growth rate, corallite structure, and stable isotopes (Knowlton et al., 1992, 1997; Van Veghel and Bak, 1993, 1994; Van Veghel et al., 1996; Lopez and Knowlton, 1997; Lopez et al., 1999; Manica and Carter, 2000; Knowlton and Budd, 2001; Pandolfi et al., 2002; Budd and Pandolfi, 2004; Fukami et al., 2004; Holcolmb et al., 2004; Levitan et al., 2004). On the basis of these characteristics, modern *Montastraea* "*annularis*" (sensu lato), long thought to represent one species, is now thought to consist of a complex of at least three sympatric species (Weil and Knowlton, 1994). These three species are best studied and differentiated in shallow- to midreef depths in Central America, and differ in overall colony shape and the shape of the growing edge. This new understanding of sibling species within the *M.* '*annularis*' complex has led to important new ways of understanding the role of niche differentiation and biotic interaction in structuring marine communities (Knowlton and Jackson, 1994).

Montastraea annularis sensu stricto forms columns, *M. faveolata* (Ellis and Solander, 1786) forms smooth, skirted mounds, and *M. franksi* (Gregory, 1895) forms bumpy, irregular mounds and plates. Morphometric analyses of nontraditional skeletal characters, including septal relief and corallite structure, show that the three species are morphologically distinct (Budd and Johnson, 1996; Knowlton and Budd, 2001; Pandolfi et al., 2002; Budd and Pandolfi, 2004). In more northern Caribbean localities, colonies from Florida appear to show the same morphological differences (Manica and Carter, 2000), but species-level morphological differences are less pronounced in the Bahamas (Budd and Pandolfi, 2004).

Not only the massive, columnar, and sheet members of the modern *Montastraea* "*annularis*" species complex have been recognized in the shallow-water Pleistocene deposits of the Caribbean Sea but also one additional form that does not live today, the organ-pipe growth form (Pandolfi and Jackson, 1997, 2001; Pandolfi et al., 1999; Pandolfi, 1999; Pandolfi and Jackson, 2001; Pandolfi et al., 2002; Klaus and Budd, 2003; Budd and Pandolfi, 2004). This organ-pipe coral is highly divergent with the modern forms, and is herein described as *Montastraea nancyi* n. sp. The purpose of the present paper is to describe and name this species taxonomically and put its occurrence into the broader context of evolutionary and ecological issues now confronting students of the *M.* "*annularis*" species complex.

MORPHOMETRIC ANALYSES

The *M.* "*annularis*" species complex is readily distinguished in the field using traditional morphological characteristics, and morphological differences exist among all species (Tables 1–3). In a series of papers using nontraditional morphological characters, Budd and her co-workers have shown that *Montastraea nancyi* n. sp. occupies a separate morphospace from both Pleistocene and modern members of the species complex (Pandolfi et al., 2002, fig. 5; Klaus and Budd, 2003, fig. 10; Budd and Pandolfi, 2004, figs. 7, 10, and 12; Holcomb et al., 2004, fig. 5). Pandolfi et al. (2002) collected the same two-dimensional size and shape coordinate data for fossil specimens (10 organ-pipe *Montastraea* [Blainville 1830] and 15 columnar *Montastraea*) from the back-reef environment of the 82 Ka reef on Barbados, and added them to the dataset already collected from 30 modern colonies of the *Montastraea* '*annularis*' species complex from Panamá. Canonical discriminant function analysis (DFA) of two-dimensional landmark data on corallites of the three living species and Pleistocene organ-pipe and columnar *Montastraea* showed divergent morphology among all taxa and morphotypes (see fig. 5 in Pandolfi et al., 2002). The two-dimensional data for the Pleistocene organ-pipe species were most similar to living *M. annularis* s.s., whereas the two-dimensional data for the Pleistocene columnar morphotype were most similar to living *M. faveolata*. Coordinates representing wall thickness, costoseptum width and length, and development of wall dissepiments differentiated the five species in the DFA. Klaus and Budd (2003) found four species of the *M.* "*annularis*" species complex from the back-reef, shallow reef-crest, and shallow forereef of the Pleistocene raised (125 Ka) reef terraces of the Dominican Republic. Key characters distinguishing the four species include wall thickness, development of the tertiary septa, corallite size, wall structure, and extensions of the costae beyond the wall. *Montastraea nancyi* had a longer and wider tertiary septum, a wider tertiary costoseptum, less-developed wall dissepiments, a greater variance in corallite diameter, and a larger budding angle than columnar growth forms in the

Table I—Distinguishing morphological characteristics of four species of the Montastraea 'annularis' species complex found in the modern and Pleistocene sequences of the Caribbean Sea.

Species	Growth form	Wall thickness (SD) and range (mm)[4]	Wall composition	Corallite diameter (SD) and range (mm)	Number of septa (SD) and range	Extension of secondary costa	Maximum Corallite spacing (SD) and range (mm)	Minimum Corallite spacing (SD) and range (mm)	Length (SD) of tertiary septa (mm)
M. annularis s.s.	Columnar	Intermediate[3]	Septothecal	2.29 (0.15) 2.1–2.6[4]	24.30 (0.79)[1]	Extensive[3]	1.93 (0.26)[1]	1.14 (0.13)[1]	0.28 (.03)[1]
M. faveolata	Massive	Thin[3]	Dissepiments	2.39 (0.15) 2.2–2.7[4]	23.83 (0.40)[1]	Extensive[3]	1.80 (0.28)[1]	0.83 (0.16)[1]	0.25 (.06)[1]
M. franksi	Plates with bumps	Thick[3]	Septothecal	2.57 (0.23) 2.4–3.4[1]	24.92 (1.44)[1]	Minor[3]	2.48 (0.34)[1]	1.28 (0.21)[1]	0.32 (.06)[1]
M. nancyi n. sp.	Organ-pipe	0.39 (0.28) 0.07–1.64[4]	Septothecal	2.49 (0.25) 2.1–3.0[2]	23.22 (1.25) 19–26[2]	0.44 (0.17) 0.15–1.12[2]	2.66 (0.77) 1.57–4.26[4]	1.01 (0.36) 0.37–2.39[4]	0.21 (.08) 0.07–0.55[4]

[1] Weil and Knowlton, 1994.
[2] Pandolfi, data from 10 colonies collected from 82 ka back-reef habitat on windward side of Barbados.
[3] Klaus and Budd, 2003.
[4] Measured from 6 corallites each from holotype and paratypes.

same strata. Type specimens from Barbados show similar features, but the length of tertiary septa was shorter (Table 1).

Budd and Pandolfi (2004) found three species in the Pleistocene terraces of the Bahamas (125 Ka) that had more morphological overlap than those found previously in Pleistocene deposits of the southern Caribbean. Despite this overlap, organ-pipe Montastraea nancyi had thin, septothecal walls with short costae, whereas wall dissepiments and costae were better developed in massive (M. faveolata) forms. Columnar growth forms (M. annularis s.s.) had intermediate wall thickness and longer costae than the other two species. Budd and Pandolfi (2004) found that relative to the three modern Panamá species, the Pleistocene species from the Bahamas overlap extensively and occupy intermediate morphospace among the modern species. In contrast, corallite morphologies of three Pleistocene Dominican Republic species match their growth form counterparts today in Panamá, and exhibit less overlap (Klaus and Budd, 2003). Budd and Pandolfi (2004) attributed this overlap and intermediacy as having been caused by past hybridization, which occurred among preexisting lineages in the Bahamas most likely in association with Pleistocene sea-level and climate fluctuations. Holcomb et al. (2004) measured internal colony-level features measured on X-radiographs with all eight characters (Table 2) showing significant differences among three modern species, Montastraea nancyi and one fossil columnar form (Table 3). DFA distinguished all species from one another.

EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE

Montastraea nancyi n. sp. was consistently as abundant as or more so than any of the other species of the M. "annularis" species complex in Barbados for the half million years before its extinction, and the same was true geographically throughout the Caribbean 125 Ka (table 5.2 in Pandolfi et al., 2001). Just like Pocillopora cf. palmata (Pandolfi et al., 2001), extinction occurred during the roughly 80,000 years between 82 Ka and Late Holocene surface outcrops when human impacts were nil. Nothing about the distribution or abundance of organ-pipe Montastraea in the fossil record foretold its demise. The geologically sudden extinction of such a widespread and abundant coral species demonstrates that natural extinction may be just as punctuated as the origin of species (e.g., Jackson and Cheetham, 1994). Such an apparent geologically rapid extinction of widespread and abundant species emphasizes the vulnerability of increasingly threatened reef coral species in the face of rapid environmental and climatic change (Pandolfi, 1999). A similar conclusion was reached for the Late Quaternary extinction of an eastern North American tree species (Jackson and Weng, 1999).

The extinction of M. nancyi coincided with measurable changes in the morphology of one of the surviving lineages of the M. "annularis" species complex. Montastraea annularis s.s. shifted toward smaller width of its columns after the extinction of M. nancyi. Moreover, assemblages of Montastraea annularis s.s. sympatric with M. nancyi throughout the duration of the latter on Barbados showed thinner column widths than those that existed in allopatry (Pandolfi et al., 2002). Pandolfi et al. (2002) attributed this morphological shift to character release, and concluded that divergent selection of morphology was maintained to decrease the effects of deleterious interspecific competition among these two closely related species. After the extinction of M. nancyi this competitive pressure was released, allowing M. annularis s.s. to grow upward at a greater rate and to exploit shallow water environments vacated by the organ-pipe M. nancyi. This exploitation allowed M. annularis s.s. to dominate living shallow water reef crest environments on Curaçao, when it was previously relegated to much lower abundances during the Pleistocene when M. nancyi dominated similar environments. Such selective pressure, attributable to biological interactions among species, is an important

TABLE 2—Internal colony-level characters measured on X-radiographs of the *Montastraea 'annularis'* species complex by Holcomb et al. (2004).

Character	Description
GROWTH	Growth rates were estimated based upon the distances between successive annual density bands.
FAN WIDTH	The widths of individual fan systems were measured in each specimen at the widest point on the fan.
CENTER-BUDDING ANGLE	Corallite budding angles were measured by placing lines parallel to the corallite wall of the mother and daughter polyps and calculating the angle of intersection for polyps near the center of each fan system.
EDGE-BUDDING ANGLE	Same as center bud, except polyps were near the edge of the fan system.
COLONY CURVATURE	Colony curvature was expressed as the ratio of the length of a line between two points on a single density band to the length of a line perpendicular to that line that connected to the highest point on the density band. This ratio was determined for the colony as a whole.
MAX ANGLE	The maximum corallite angle was determined by measuring the angle of intersection of a line parallel to the growth axis and a line parallel to the corallite wall of the corallite angled the furthest from the growth axis (from Graus and Macintyre, 1982).

consideration in the interpretation of evolutionary mechanisms in marine invertebrates.

SYSTEMATIC PALEONTOLOGY
Family FAVIIDAE
Genus MONTASTRAEA Blainville, 1830
MONTASTRAEA NANCYI new species
Figures 2–6

Diagnosis.—Branching colonies are formed by long, thin pipes or columns. Septothecal walls are 0.07–1.6 mm in thickness. Corallites are typically 2.1–3.0 mm in diameter with maximum spacing between corallites ranging from 1.57–4.26 mm and minimum spacing ranging from 0.37–2.39 mm. Extension of secondary costae ranges between 0.15 and 1.12 mm. Length of tertiary septa is 0.07–0.55 mm. Septa are normally in three complete sets with the number of septa ranging from 19 to 26. X-radiographs reveal high growth rates between 8.6 and 16.5 mm/yr, intermediate fan widths ranging between 12 and 120 mm, and small center (5–11°) and edge (5–14°) budding angles.

Description.—Colonies have a distinct organ-pipe growth form, whereby slender branches rise from a common massive base. Mature colonies resemble a huge "pincushion" from which protrude numerous, closely set club-shaped pins. These pins or pipes have a mean width ranging from 8–15 cm. Pipes generally show little difference in the preservation of surficial corallites between their tops and sides, indicating that all polyps were alive simultaneously during life. Colonies may be several meters in diameter and up to 2 m in height.

Etymology.—The species is named for Drs. Nancy Budd and Nancy Knowlton, who have spent a large part of their very successful careers studying various evolutionary aspects of the *Montastraea "annularis"* species complex.

Types.—Holotype, USNM 1098634 (AFO-111); paratypes USNM 1098635 (AEO-207), USNM 1098636 (AFO-104), USNM 1098637 (AFO-105), USNM 1098638 (AFO-106), USNM 1098639 (CC-121), USNM 1098640 (CC-124), USNM 1098641 (CC-130), USNM 1098642 (D-096), USNM 1098643 (D-102). All types are from the Pleistocene raised reef terraces of Barbados (Table 4).

Occurrence.—Pandolfi et al. (2001) documented the distribution and abundance of *M. nancyi* throughout the Pleistocene of the Caribbean Sea (Fig. 1). Reports from other workers include the 125 Ka raised reef terraces on Curaçao (Pandolfi and Jackson, 2001), San Andrés, Providence Island, Barbados (Mesolella, 1968), the Bahamas (Budd and Pandolfi, 2004), Key Largo, Florida (Pandolfi and Budd, personal data), Grand Cayman Island (Hunter and Jones, 1996), and the Dominican Republic (Geister, 1982; Klaus and Budd, 2003). *Montastraea nancyi* had a broad and oceanic Caribbean distribution (Fig. 1), but its true geographic range may have been greater owing to its very recent recognition. So far, reports of the species are almost exclusively oceanic, so it may have favored insular settings.

Quantitative censuses of Pleistocene reef coral communities have been taken from the 125 Ka terrace (when sea level was 2–6 m higher than present) from many localities around the Caribbean, including Key Largo Florida, San Andrés, Curaçao, the Bahamas, and Barbados (Pandolfi and Jackson, 1997, 2001, 2006; Greenstein et al., 1998; Pandolfi, 2001a). From these censuses it is clear that organ-pipe *Montastraea nancyi* had a very broad ecological range in shallow water, from protected back-reef areas behind barrier reef crests to leeward and windward reef-crest habitats. Populations of *Montastraea nancyi* often dominated these different reef habitats, especially in areas of low to medium wave energy. It was the dominant species in the Pleistocene back-reef environment of Key Largo and Curaçao and was co-dominant with the Elkhorn coral *Acropora palmata* (Lamarck, 1816) in the Pleistocene leeward reef crest of Curaçao and San Andrés. *Montastraea nancyi* was also locally abundant throughout the 500 + Ka Pleistocene history of reef growth in Barbados (Mesolella, 1968; Pandolfi, 2001b).

The fossil record of *Montastraea nancyi* ranges back to the

TABLE 3—Distinguishing morphological characteristics derived from X-radiographs of four species of the *Montastraea 'annularis'* species complex found in the modern and Pleistocene sequences of the Caribbean Sea (from Holcomb et al., 2004). Pooled mean values among Caribbean sites are shown with SD and ranges.

| Species	Growth rates (SD) and range (mm/yr)	Corallite fan width (SD) and range (mm)	Center-budding angle (SD) and range (°)	Edge-budding angle (SD) and range (°)	Colony curvature (SD) and range	Max angle (SD) and range (°)
M. annularis s.s.	10.1 (2.6) 6.2–16.8	109 (50) 9–210	8 (2) 4–13	10 (2) 7–14	0.27 (0.10)	120 (27) 84–175
M. faveolata	8.6 (2.5) 4.4–12.4	44 (11) 26–61	11 (2) 8–16	13 (2) 11–17	0.25 (0.14)	95 (14) 68–118
M. franksi	4.1 (2.1) 0.9–10.3	62 (41) 23–216	17 (5) 9–30	19 (5) 6–27	0.16 (0.06)	84 (27) 14–134
M. nancyi n. sp.	12.6 (2.1) 8.6–16.5	66 (27) 12–120	8 (1) 5–11	9 (2) 5–14	0.21 (0.08)	75 (12) 53–108
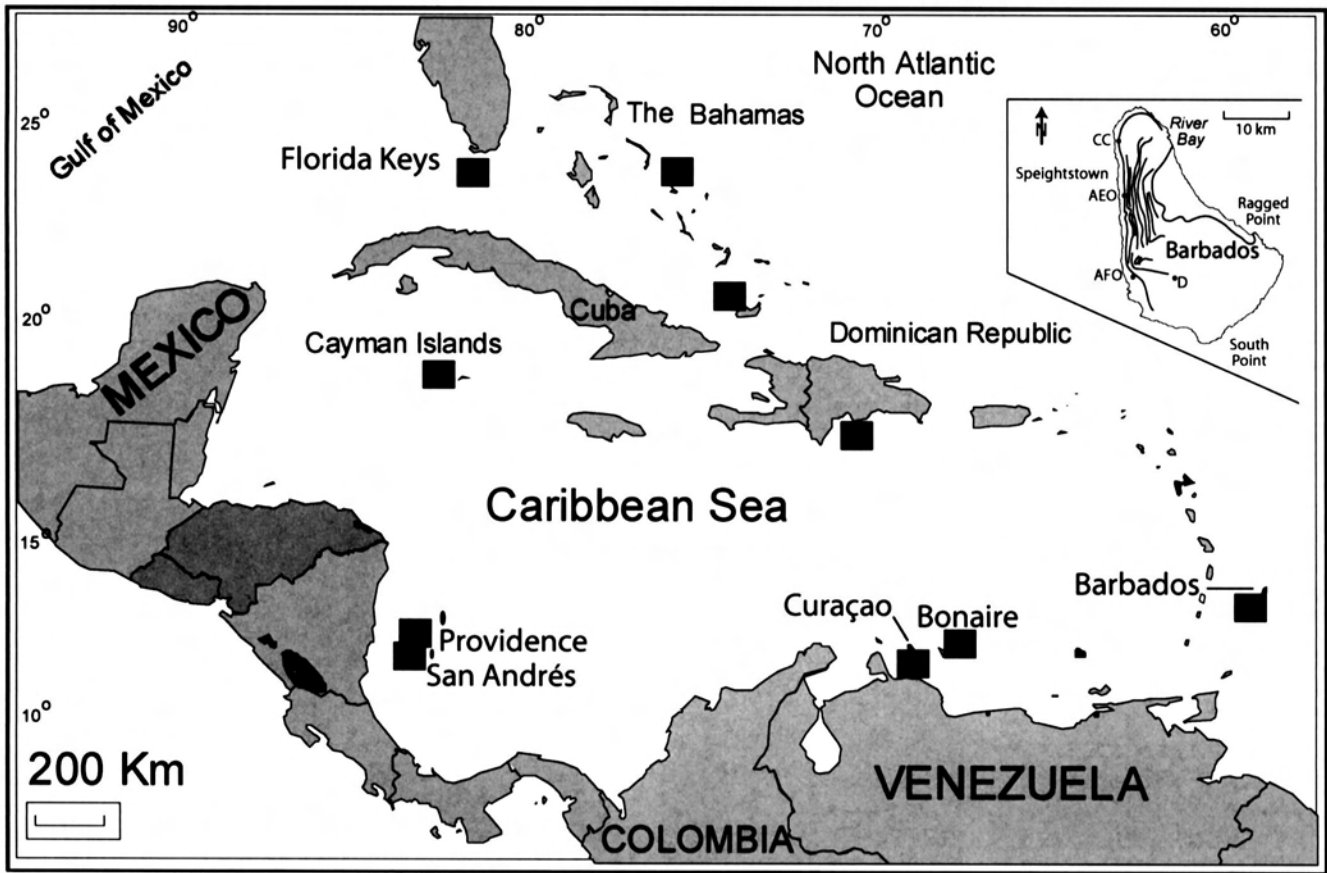
FIGURE *1*—Known occurrences of *Montastraea nancyi* n. sp. throughout the Pleistocene reefs of the Caribbean Sea. Occurrences depicted as filled boxes. Inset is type localities on Barbados (see also Table 4).

oldest terraces on Barbados, at least 600 Ka and extending forward to 82 Ka. Its closest relatives are undoubtedly other members of the *M.* "*annularis*" complex, which extend back to the middle Miocene, including three thin-columned species of *Montastraea* "*limbata*" (Budd and Klaus, 2001). Phylogenetic analyses have yet to be made, but there is clearly no dearth of possible Caribbean ancestors.

Discussion.—The extinct organ-pipe form has a different morphology from the living species of the *Montastraea* "*annularis*" species complex. Recent columnar *M. annularis* s.s. usually has much broader columns that diverge from one another throughout colony development. These colonies commonly attain diameters and heights of up to 3 m and have been described throughout the Caribbean, including the Cayman Islands (Hunter and Jones, 1996), Jamaica (Dustan, 1975; T. Goreau, personal commun. 1999), Honduras (Knowlton et al., 1997), Panama (Knowlton et al., 1992), Bonaire (Scatterday, 1974), and Barbados (Lewis, 1960; Pandolfi, personal data). Narrow columns more suggestive of the fossil organ-pipe species than typical *M. annularis* s.s. can also develop, but their mode of formation is usually different.

Such narrow branches usually form as a result of the dying back of originally large columns, and they do not extend very far back towards the base of the colony. Scatterday (1974) described this process in *M. annularis* s.s. from Bonaire. Based on comparative taphonomy, *Montastraea nancyi* had living corallites along the margins of the columns or pipes (very little bioerosion along column margins), whereas living and fossil columnar *Montastraea* have sides of columns with senescent and highly bioeroded corallites, respectively (Pandolfi et al., 2002).

X-radiograph measurement of colony characters in *Montastraea nancyi* revealed the highest growth rates, single corallite-fan systems with greater width than *M. faveolata* and *M. franksi* but less curvature than *M. annularis* and *M. faveolata* (Table 3). Budding angles for *M. nancyi*, along with *M. annularis* and *M. faveolata* were smaller than for *M. franksi*. The larger and more variable budding angles observed in X-rays of *M. franksi* are consistent with the uneven calice distribution and greater spacing reported for this species (Budd, 1993; Van Veghel and Bak, 1993; Szmant et al., 1997).

TABLE *4*—Locality information for holotypes and paratypes of *Montastraea nancyi* found in the Pleistocene sequences of Barbados.

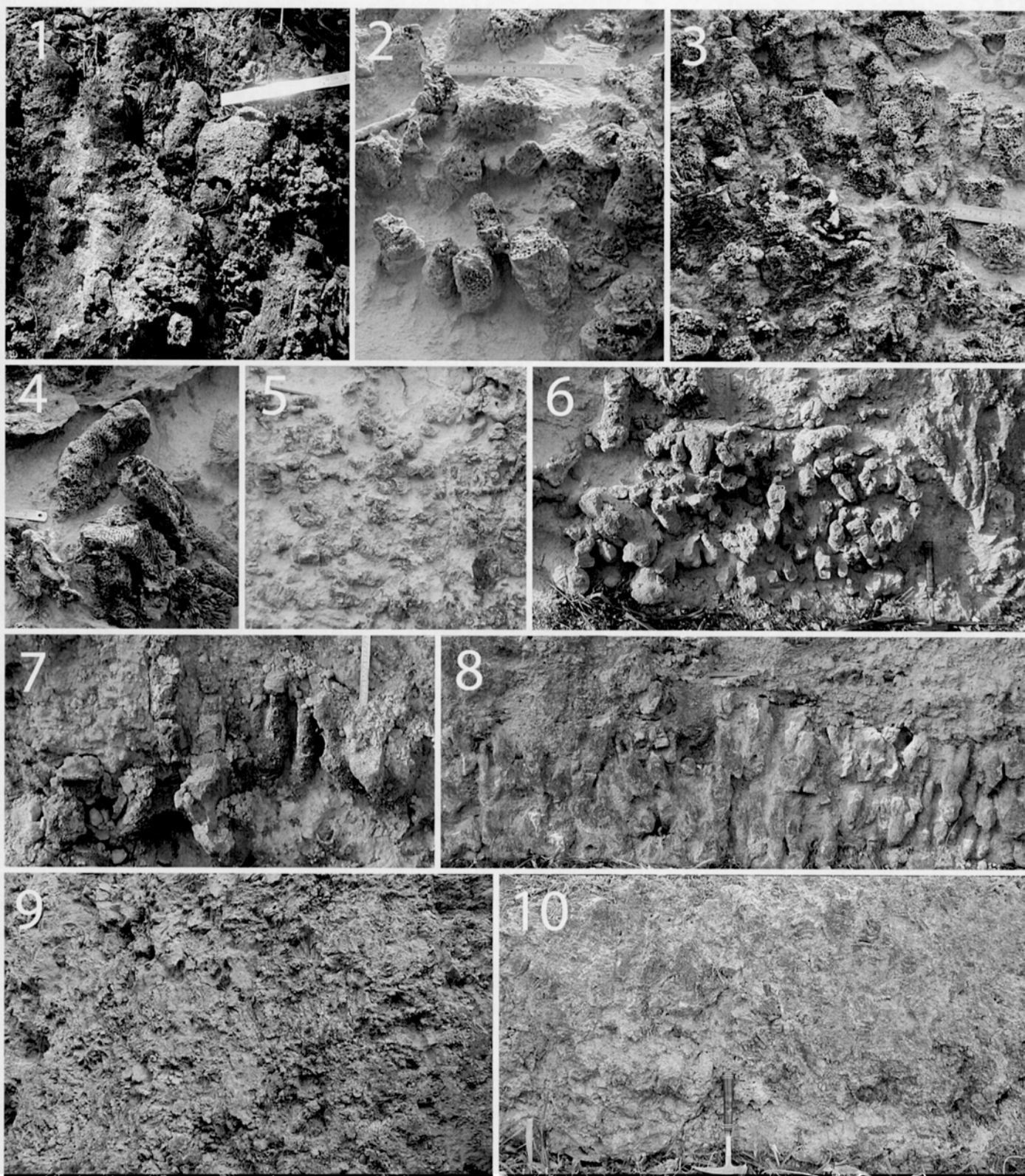| Locality[1]	Elevation (m a.s.l.)	Age (ka)	Terrace	Location	Lat (N)	Long (W)
AEO	37	125	Rendezvous Hill	NW Coast	13°13.54′	59°38.31′
AFO	80	195	Durants	Clermont Nose	13°8.00′	59°39.38′
CC	61	125	Rendezvous Hill	NW Coast	13°15.56′	59°37.79′
D	90	320	Dayrells	St. George's Valley	13°8.22′	59°35.00′

[1] Mesolella 1968.

FIGURE 2—Field photos of holotype (AFO-111) and all paratypes of *Montastraea nancyi* n. sp. from the Pleistocene windward terraces of Barbados. *1*, USNM 1098635, Locality AEO; *2*, USNM 1098636, Locality AFO; *3*, USNM 1098637, Locality AFO; *4*, USNM 1098638, Locality AFO; *5*, USNM 1098634, Locality AFO; *6*, USNM 1098639, Locality CC; *7*, USNM 1098640, Locality CC; *8*, USNM 1098641, Locality CC; *9*, USNM 1098642, Locality D; *10*, USNM 1098643, Locality D.
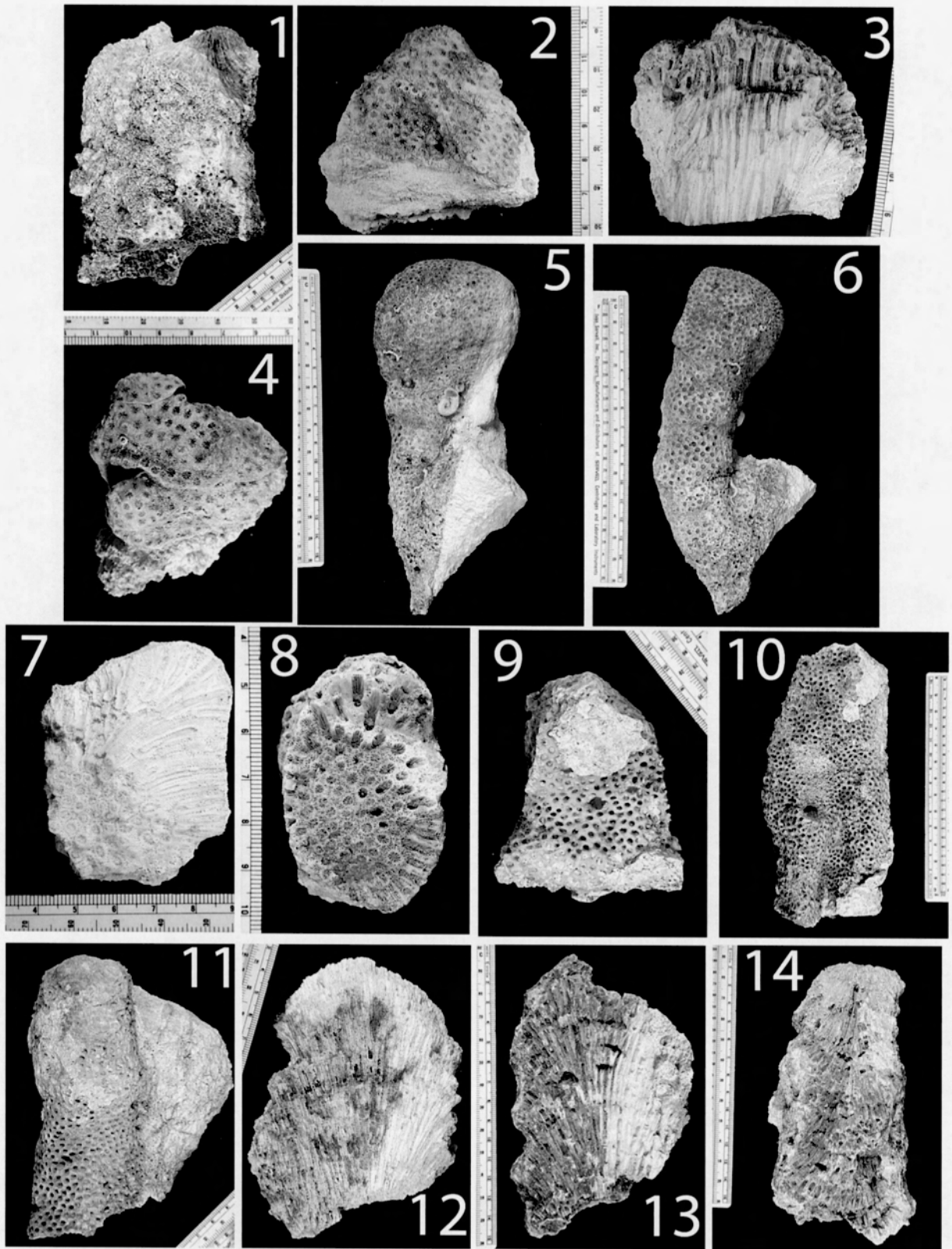
FIGURE 3—Columns of holotype (USNM 1098634) and all paratypes of *Montastraea nancyi* n. sp. from the 82 Ka back-reef setting of Barbados. *1*, USNM 1098635; *2, 3*, USNM 1098636; *4*, USNM 1098637; *5, 6*, USNM 1098638; *7*, USNM 1098634, Locality AFO; *8*, USNM 1098639; *9, 10*, USNM 1098640; *11*, USNM 1098641; *12*, USNM 1098642; *13, 14*, USNM 1098643. Localities as in Figure 2.
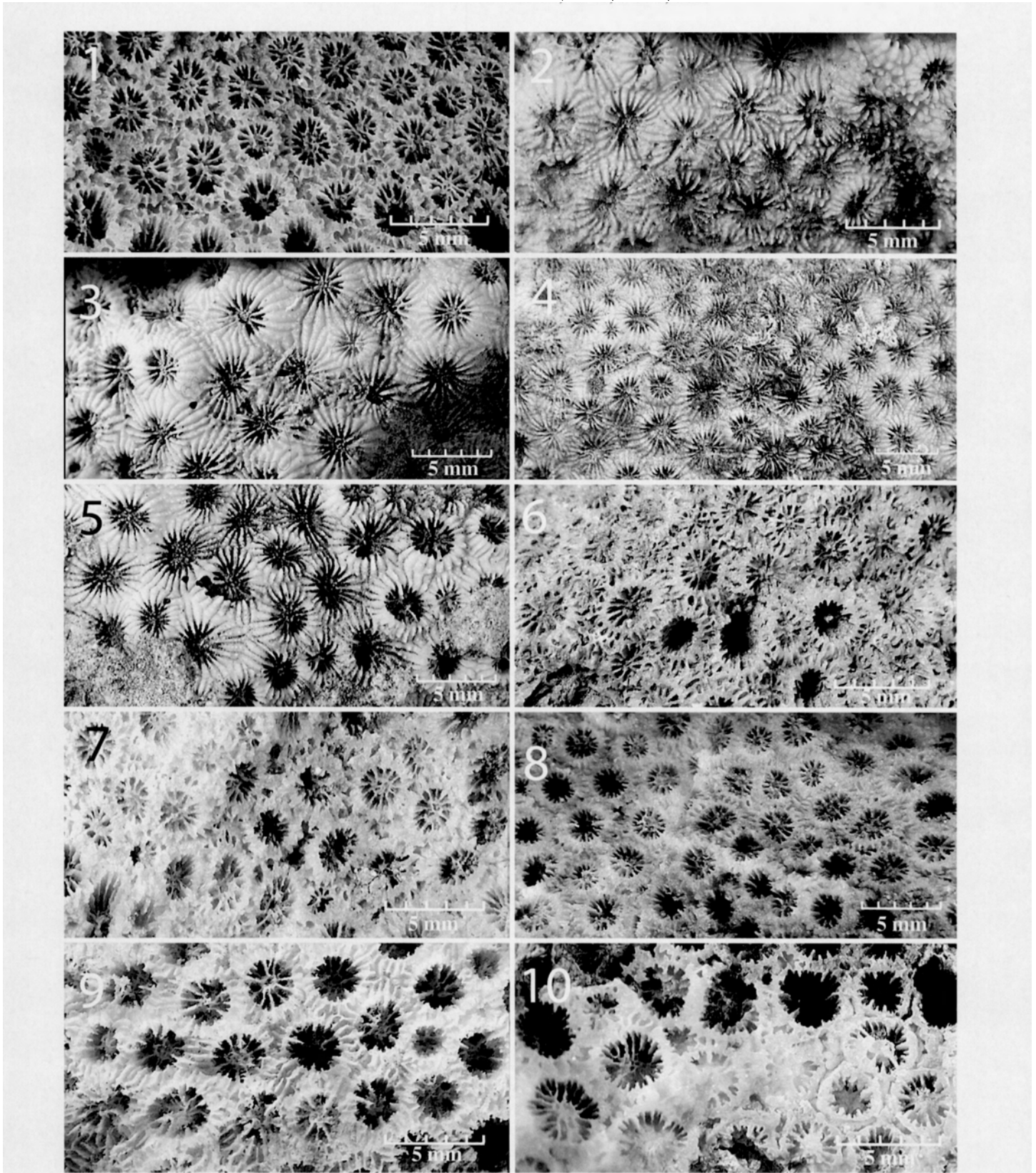
FIGURE 4—Close-up colony surfaces of holotype (USNM 1098634) and all paratypes of *Montastraea nancyi* n. sp. from the Pleistocene windward terraces of Barbados. *1*, USNM 1098635; *2*, USNM 1098636; *3*, USNM 1098637; *4*, USNM 1098638; *5*, USNM 1098634; *6*, USNM 1098639; *7*, USNM 1098640; *8*, USNM 1098641; *9*, USNM 1098642; *10*, USNM 1098643. Localities as in Figure 2.
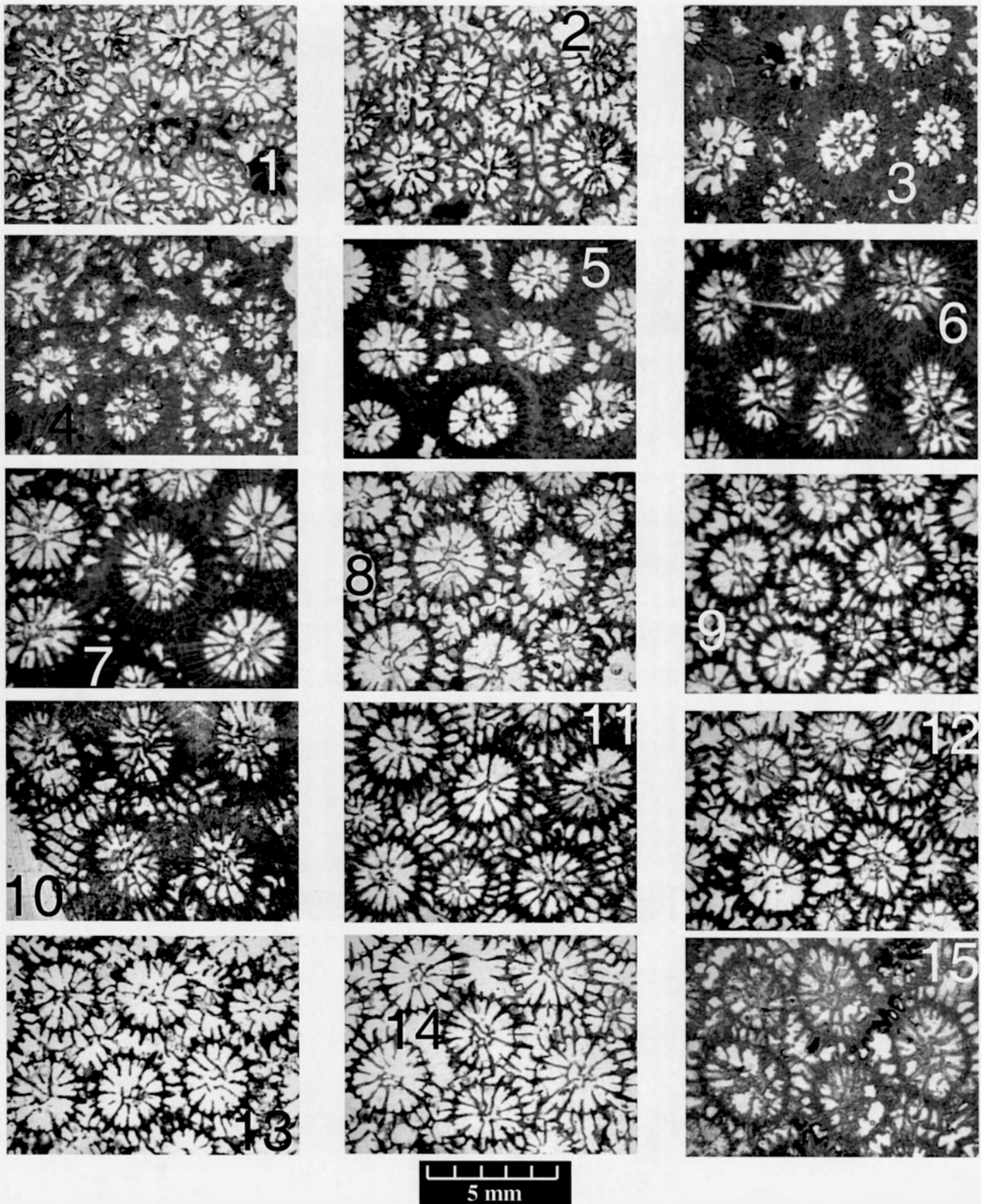
FIGURE 5—Transverse sections of holotype (USNM 1098634) and all paratypes of *Montastraea nancyi* n. sp. from the Pleistocene windward terraces of Barbados. *1, 2,* USNM 1098635; *3–5,* USNM 1098636; *6, 7,* USNM 1098637; *8,* USNM 1098638; *9,* USNM 1098634; *10, 11,* USNM 1098639; *12,* USNM 1098640; *13, 14,* USNM 1098642; *15,* USNM 1098643. Localities as in Figure 2.
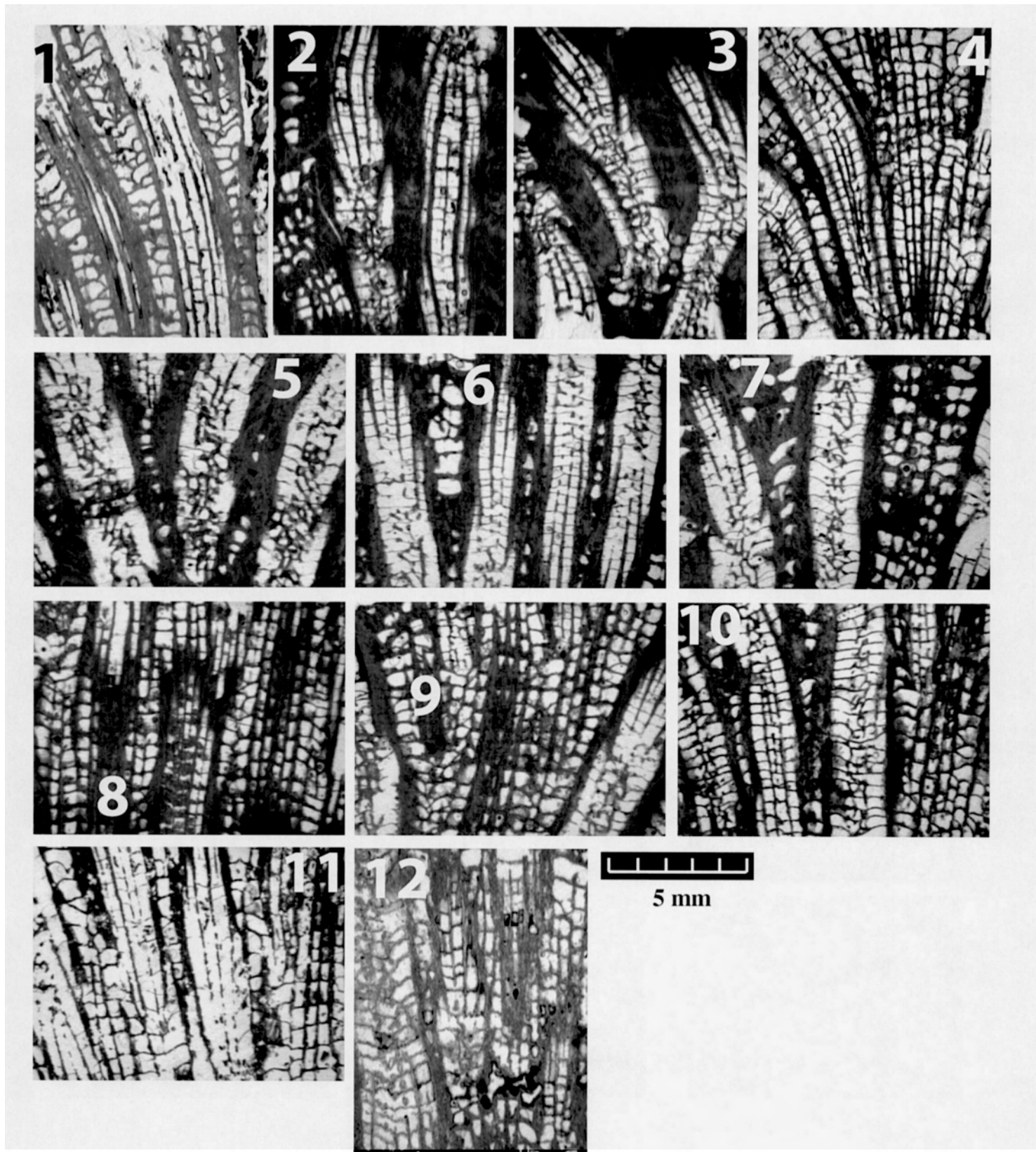
FIGURE 6—Longitudinal sections of holotype (USNM 1098634) and all paratypes of *Montastraea nancyi* n. sp. from the Pleistocene windward terraces of Barbados. *1*, USNM 1098635; *2*, *3*, USNM 1098637; *4*, USNM 1098639; *5–7*, USNM 1098636; *8*, USNM 1098638; *9*, USNM 1098634; *10*, USNM 1098640; *11*, USNM 1098642; *12*, USNM 1098643. Localities as in Figure 2.

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