

NOMENCLATURE AND BIOLOGY OF *ASTRANGIA POCULATA*  
(=*A. DANAEE*, =*A. ASTREIFORMIS*)  
(CNIDARIA: ANTHOZOA)

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*Abstract.* — The encrusting to ramose northern star coral, *Astrangia poculata*, is a common inhabitant of rocky shorelines, jetties, and pilings along the north-west Atlantic and Gulf of Mexico coastlines of the United States. Despite its popularity as an experimental laboratory animal, there has been considerable confusion as to the number of species which may exist and the proper name(s) of the species. A reexamination of material from throughout this range confirms that there is only one species, the correct name of which is *Astrangia poculata* (Ellis & Solander, 1786). A neotype has been deposited in the National Museum of Natural History. The same neotype is also deposited as the type of *A. michelinii* Milne Edwards & Haime 1849, type species of *Astrangia*.

The genus *Astrangia* includes over 30 Recent nominal species within the family Rhizangiidae, and is represented by 20 fossil species, some of which lived as early as the Middle Cretaceous, approximately 100 million years ago (Wells 1956). Members of the genus are all relatively small and are usually insignificant components of the fauna where they occur. The various species of *Astrangia*, however, collectively occupy a vast geographic range, possibly broader than that of any other genus of coral.

Unfortunately, the genus *Astrangia* has never been completely reviewed. It is probable that many species names are synonyms, and also that a number of yet undiscovered species may exist (Pilson 1975). The confusion that exists within this genus became evident when a group of scientists at the University of Rhode Island began a series of studies on the ecology, physiology, and life history of the coral found in Narragansett Bay. Whereas several previous studies had referred to the northern star coral as *Astrangia danae*, a number of other papers had been published on the very sim-

ilar *Astrangia astreiformis* from the southeastern coasts of the United States. However, other texts suggested that only one species of *Astrangia* existed along the entire North Atlantic and Gulf coasts of North America (Hyman 1940, Wells 1956, for reviews see Cummings 1983, and Jaap, in prep.). *A. astreiformis* was also reported to occur off the west coast of Africa (Thiel 1928, Chevalier 1966).

Throughout its range, the northern star coral appears remarkably tolerant of a wide range of environmental conditions. Colonies of *Astrangia* are generally considered to be ahermatypic (non-reef-building) and hence azooxanthellate (=asymbiotic, i.e., lacking zooxanthellae), but some colonies of the northern star coral contain these algal cells abundantly within their tissues (Boschma 1925a). These two factors, adaptability and variability in algal symbiosis, have contributed to the increasing popularity of this coral as an experimental laboratory animal. Therefore, in order to aid future researchers, we were motivated to clarify the taxonomic status of this coral.

## Family Rhizangiidae d'Orbigny, 1851

Genus *Astrangia* Milne Edwards  
& Haime, 1848a

*Diagnosis.*—Colonial, usually azooxanthellate. Colonies encrusting or subplocoid, formed by extratentacular budding from edge zone; corallites united basally by thin coenosteum; septa dentate; columella papillary. [Type species: *A. michelinii* Milne Edwards & Haime, 1848b, by monotypy (= *A. poculata* Ellis & Solander, 1786).]

*Astrangia poculata*  
(Ellis & Solander, 1786)  
Figs. 1–6

“Stony coral found on the shore near New York.”: Ellis, 1755:84, pl. 32, figs. A.1, A.3.

?*Madrepora calycularis* Pallas, var.  $\beta$ , 1766: 319 note 186B.—Esper, 1790:283.

*Madrepora poculata* Ellis & Solander, 1786: 165.—Gmélin, 1791:3766.—Esper, 1790: 283 (= *M. calycularis*  $\beta$ ). [Original type locality “near New York.” Type specimen lost (P. F. S. Cornelius, pers. comm.). Type locality (neotype) “off Atlantic City, New Jersey.” Neotype deposited in the National Museum of Natural History USNM 80350.]

*Madrepora porculata*: Turton, 1806:623 [Misspelling of *poculata*].

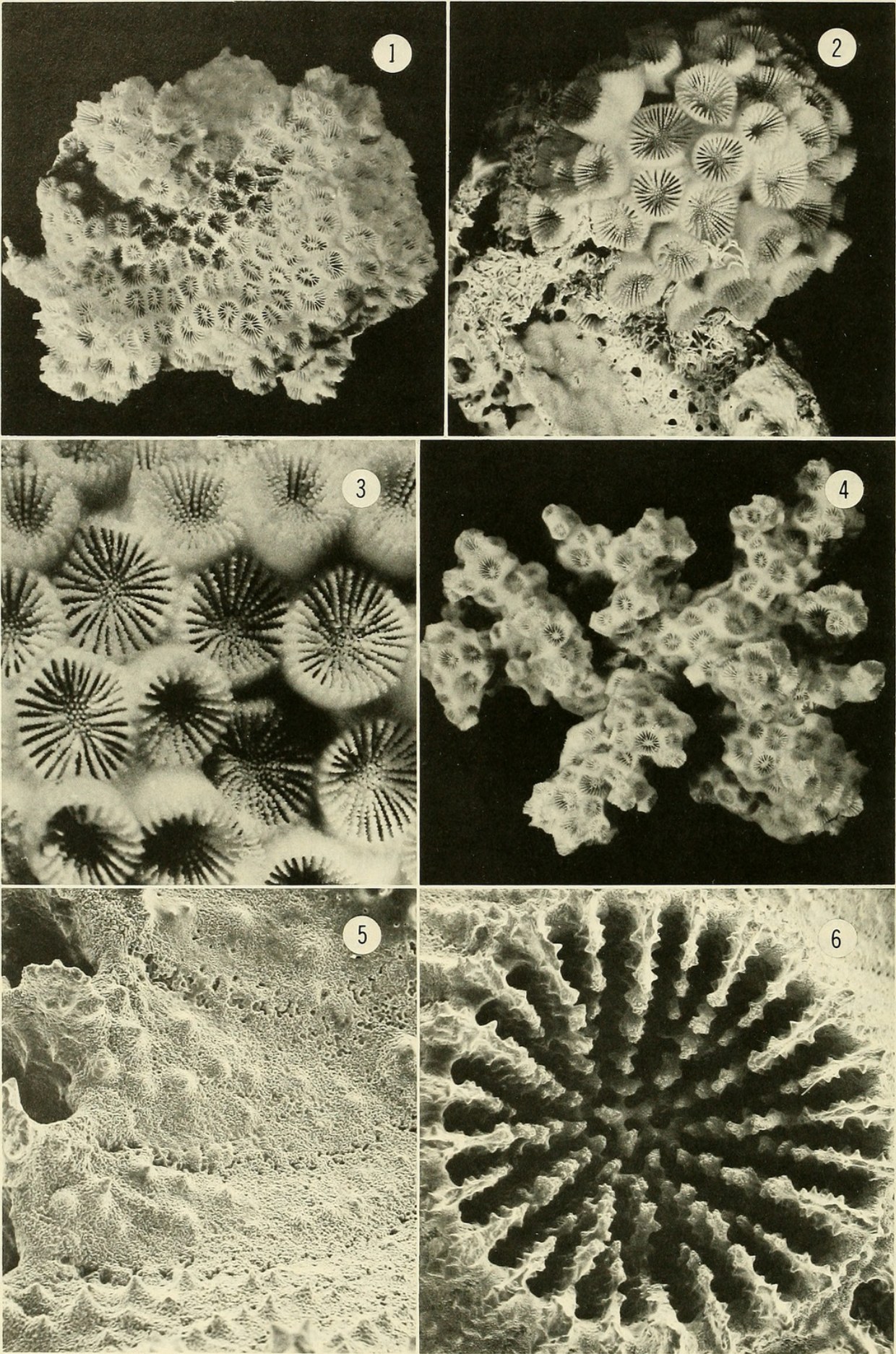
*Astrangia michelinii* Milne Edwards & Haime (ME & H), 1848b:320, pl. 7, fig. 5, 5a; 1857:614. [Type of the genus. Original type locality unknown. Type specimen last seen by Wells in 1934, Coll. Michelin No. 412. Type lost (Chevalier, 1966). Type locality (neotype) “off Atlantic City, New Jersey.” Neotype deposited in the USNM, USNM 80350.]

*Astrangia michelini*: ME & H, 1849:181; 1850:xliv (cited as the type species).—Verrill, 1866a:324.—Vaughan, 1901: 299.—Vaughan & Wells, 1943:177.—Alloiteau, 1952:623 (= *A. danae* Agassiz 1850).—Chevalier, 1966:930 (= ?*A. astreiformis* ME & H 1849).—Wells,

1986:6 (cited as the type species). [Emended spelling of *A. michelinii*.]

*Astrangia danae* ME & H, 1849:180.—Verrill, 1863:40; 1864:47 (not *A. danae* Agassiz 1850); 1866a:324 (= *A. edwardsii*); 1866b:335; 1872:432–438; 1874:446 (geography).—Pearse & Wharton, 1938: 636.—Cairns, 1979:207.—Jacques & Pilson, 1980:167–178 (physiology, symbionts, Rhode Island).—Szmant-Froelich, 1980a:1–191 (natural history, biochemistry, Rhode Island).—Szmant-Froelich & Pilson, 1980:85–97 (feeding frequency, biochemistry, Rhode Island).—Szmant-Froelich, 1981:133–144 (nutrition, Rhode Island).—Cummings, 1983:1–147 (physiology, morphology, Rhode Island, Florida).—Peters, 1984:61–63, figs. 6b, c, d, 10d, e, 13g, 17a, b, 22h, 26f, g (histology, Rhode Island).—Wiseman, 1984:1–75 (biochemistry).—Peters & Pilson, 1985:215–230 (sedimentation stress, histopathology, Rhode Island). [Type locality unknown. Type specimen last seen by Wells in 1934, now missing from Coll. Michelin (Cairns 1981).]

*Astrangia astreiformis* ME & H, 1849:181.—Verrill, 1864:47; 1866a:324.—Vaughan, 1901:300, pl. II, figs. 2, 2a, 2b (Puerto Rico).—Whitten et al., 1950:75 (Texas channels).—Parker, 1959:2130, 2131, fig. 19a; 1960:317, 334, pl. 3, fig. 23 (inlet and deep channel assemblage, common on shell, Texas).—Richmond, 1962:69 (Mississippi).—Wells et al., 1964:566, 581 (on scallop shells, North Carolina).—Macintyre & Pilkey, 1969:374–375 (off North Carolina).—Macintyre, 1970: 178.—Pampe, 1971:399, pl. 2, fig. 7.—Defenbaugh, 1976:27, 37, pl. 5f, fig. 53.—Cairns, 1977:5; 1978:10 (east, west and southwestern Gulf of Mexico, 10–29 m); 1981:10, fig. 12 (systematics: = *A. danae* Agassiz 1850 not *A. danae* ME & H 1849).—Cooley, 1978:8, 86 (Pensacola, Florida, estuary).—Fotheringham et al., 1980:17, 103, fig. 2.25.—Brunet, 1982:1–150 (feeding behavior, growth and sur-



- vival, Texas).—St. Pierre, 1986:1–55 (reproduction, Texas). [Type locality “United States.” Type found by Wells in Paris in Coll. Michelin in 1934, but not found by Chevalier in 1980 (Cairns 1981).]
- Astrangia danae* Agassiz, 1850:68–77, pl. I, fig. 7 (feeding behavior, digestion, colony growth, new polyp formation, nematocyst function, Massachusetts).—Verrill, 1863:40 (North Carolina); 1864:47 (= *A. astreiformis* in Leidy, 1855, not *A. danae* ME & H 1849); 1866a:324 (not *A. danae* ME & H 1849); 1866b:335; 1872:436, 437 (= *A. astraeiformis* ME & H 1849); 1873:408; 1874:446 (Vineyard Sound and adjacent waters).—Agassiz & Agassiz, 1865:16, figs. 16–20.—Pourtalès, 1871:80.—Dana, 1872, 1890:67–68, figured p. 68, a, b, c.—Damon, 1882:221.—Fewkes, 1889:7–10, pls. 1–5 (natural history illustrations); 1891:53.—Hargitt, 1914:250, pl. 43, fig. 9 (natural history, Casco Bay, Maine).—Boschma, 1925a:65–67 (zooxanthellae symbiosis); 1925b:407–439 (feeding behavior, digestion, zooxanthellae symbiosis).—Cowles, 1930:333 (Chesapeake Bay, Cape Henry, Cape Charles).—Pratt, 1935:159, fig. 239.—Pearse, 1936:178.—Richards & Harbison, 1942:178, pl. 22, figs. 2 & 3 (Miocene, New Jersey).—Vaughan & Wells, 1943:177 (see footnote 52: =? *A. michelini* ME & H 1848).—Field, 1949:6, 18, pl. I, fig. 7.—Waterman, 1950:127–131, fig. pp. 120–121 (structure of corallum and polyps, zooxanthellae, feeding, reproduction).—Alloiteau, 1952:623, fig. 74 (= *A. michelini* ME & H 1848).—Hand, 1964:25, pl. 3, fig. 4 (description).—Driscoll, 1967:633–641.—Robertson et al., 1970:55–65.—Calder, 1972:101 (Chesapeake Bay, Hog Island and Eastern Shore).—Sassaman & Mangum, 1973:1313–1319 (anaerobic metabolism).—Jacques et al., 1977:455–461 (physiology, calcification, Rhode Island).—Hayes & Goreau, 1977:26–40 (calcification, histology).—Bachand, 1978:283–284 (habitat, life history).—Calder & Hester, 1978:93 (Charleston, South Carolina).—Weston, 1980:1–93 (zooxanthellae distribution, Chesapeake Bay). [Type locality “Massachusetts.” Deposition unknown.]
- Astrangia astraeiformis*: ME & H: Leidy, 1855:139–140, pl. 10, figs. 9–16 (synonymy, nematocysts, Rhode Island). [Misspelling of *A. astreiformis* ME & H 1849].
- Astrangia astraeiformis*: ME & H: ME & H, 1857:614.—Verrill, 1863:39; 1866a:324; 1866b:335; 1872:436 (= *A. danae* Agassiz 1850).—Pourtalès, 1871:80.—not Thiel, 1928:283–285, pl. 2, fig. 22 (= *A. mercatoris* Thiel 1941, West Coast of Africa).—Thiel, 1941:5, 15, pl. 1, figs. 5–6 (Martinique).—Pearse & Williams, 1951:136 (incorrectly attributed to Leidy, 1855, Maine to Florida and the West Indies).—Chevalier, 1966:926–930, pl. 3, figs. 2–3, pl. 4, fig. 6 (synonymy, description, Sierra Leone, Africa). [Misspelling (or corrected spelling) of *A. astreiformis* ME & H 1849.]
- Astrangia danai*: ME & H, 1857:614. [Misspelling (or corrected gender) of *A. danae* ME & H 1849.]
- Astrangia edwardsii* Verrill, 1866a:324 (=nom. nov. for *A. danae* ME & H 1849, see Remarks); 1866b:335.
- not *Astrangia mercatoris* Thiel, 1941:16–17, pl. 2, fig. 1 (= *A. astraeiformis* Thiel, 1928:283–285, pl. 2, fig. 22; Angola, Bay of Elephants, West Coast of Africa).—

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Figs. 1–6. *Astrangia poculata*: 1, Neotype colony (off Atlantic City, New Jersey, USNM 80350),  $\times 0.88$ ; 2–3, Colony from off Jacksonville, Florida, 15 m, USNM 78509,  $\times 1.20$ ,  $\times 3.40$ , respectively; 4, Deep-water branched colony (off Western Dry Rocks, Sand Key, Florida, 263 m, USNM 78508),  $\times 0.86$ ; 5, SEM of coenosteum adjacent to calice showing lines of perforations constituting intercostal striae and coenosteal granules,  $\times 49$ ; 6, SEM of calice with 24 septa,  $\times 23$  (5–6, R/V Gerda station 1002, USNM 78507).

- Chevalier, 1966:929–930 (discusses synonymy, see Remarks).
- Astrangia astraeiformis*: no authority cited: Hedgpeth, 1953:164 (Texas). [Misspelling of *A. astreiformis*.]
- not *Astrangia astraeiformis*: no authority cited: Buchanan, 1954:85–86 (= *A. astraeiformis* Thiel 1928 = *A. mercatoris* Thiel 1941, Ivory Coast, French Congo, Angola, Africa). [Misspelling of *A. astreiformis*.]
- Astrangea danae*: no authority cited: Goreau & Bowen, 1955:1188 (calcification). [Misspelling of *Astrangia danae*.]
- Astrangia astreiformis*: Milne Edwards & Haines (sic): Pampe, 1971:399, pl. 2, fig. 7 (Pleistocene, Texas). [Misspelling, spelled *A. astreiformis* later on same page.]
- Astrangia asteriformis*: no authority cited: Rudloe, 1971:154–157, 167, 172–174, figured on p. 174 (natural history, hardness in aquarium, Florida). [Misspelling.]
- Astrangia astreiformis*: no authority cited: Ladd, 1951:137, 139, 149 (Texas coastal waters).—Stephenson & Stephenson, 1952:35 (distribution, taxonomy).—Hedgpeth, 1953:164 (Texas).—Gunter & Geyer, 1955:40, 44, 45, 56, 57, 65 (Texas, Louisiana).—Parker, 1956:310, 315, 329, 354, 370 (dead specimens collected in east Mississippi delta region).—Courtney & Edmond, 1974:63 (Marco Island, Florida).—Fotheringham & Brunenmeister, 1975:36, 161, fig. 2.24 (natural history).
- Astrangia danae*: no authority cited: Wilson, 1900:350 (North Carolina).—Allee, 1923:176 (Woods Hole, Buzzards Bay, and Vineyard Sound, Massachusetts).—Hyman, 1940:610–611 (morphology, natural history).—Storer, 1951, figured on p. 321.—Stephenson & Stephenson, 1952:35 (distribution, taxonomy).—Blake, 1953:23 (Pleistocene, Maryland).—Zinn, 1964:15 (Rhode Island).—Goreau et al., 1971:254.—Williams & Murdoch, 1973:551–563 (effects of gamma radiation on).—Cummings, 1976:1–115 (physiology, Rhode Island).—Szmant-Froelich & Pilson, 1977:417–424 (nitrogen excretion, symbiosis, Rhode Island).—Hoffman et al., 1978:165–170.—Jacques, 1978:1–169 (calcification).—Gosner, 1979:93–94, fig. 20.—Storer et al., 1979, figured on p. 320, 372, 390.—Szmant-Froelich, 1980b:1–3 (popular account).—Szmant-Froelich et al., 1980:257–269 (reproduction, Rhode Island).—Meinkoth, 1981:391.—Cummings & McCarty, 1982:1125–1129 (calcification, stable carbon isotopes, Rhode Island).—Jacques et al., 1983:135–148 (ecology, metabolism, Rhode Island).—Swart, 1983:72 (stable carbon isotopes).—Szmant-Froelich & Pilson, 1984:153–162 (feeding frequency, nitrogen metabolism, respiration, Rhode Island).
- Astrangia* sp.: Ferguson, 1948:17 (salinity tolerance, Louisiana).—Keith & Weber, 1965:500 (isotopic composition, calcification, in part: Woods Hole, Massachusetts).—*not* Rabalais, 1978:62 (= *Oculina diffusa*, Gulf of Mexico).
- Diagnosis*.—Encrusting, massive, or ramose irregularly shaped colonies. Corallum cerioid to plocoid, new polyps produced by extratentacular budding, having corallites united basally by thin peritheca (vesicular coenosteum). Corallites round, irregular, or polygonal; tightly packed or spaced several millimeters apart, highly variable even within a single specimen. Calices 1–7 mm in diameter, with distinct equal costae on many corallites. Septa hexamerally arranged in 4 cycles, however, complete fourth cycle (48 septa) only attained in very large calices. Most calices have 24 septa, the  $S_3$  merging basally with the  $S_2$  about  $\frac{3}{4}$  distance to columella. With increase in calicular diameter, pairs of  $S_4$  form flanking some  $S_3$ , often with one pair per system (the space between two  $S_1$ ) resulting in 36 septa. Complete fourth cycle (48 septa) attained only in calices over 6 mm in diameter. Septa

strongly dentate, particularly  $S_3$  at region of  $S_4$  fusion, and slope gradually toward columella. Fossa shallow. Columella trabecular or papillose.

Polyps up to 1 cm tall and translucent white (azooxanthellate = asymbiotic) to brown (zooxanthellate = symbiotic, see Schuhmacher & Zibrowius 1985, for review of this terminology). Numerous nematocyst batteries on surface of tentacles; tip of tentacle rounded. Directive mesenteries present. Corallum often invaded by endolithic red or green boring algae, burrowing polychaetes, or sponges (e.g., *Cliona celata* Grant, see Cummings 1983).

Cnidocyst batteries principally composed of spirocysts. Terminal knob packed with large microbasic-p-mastigophore nematocysts (about  $29\ \mu\text{m}$  long  $\times$   $8\ \mu\text{m}$  in diameter in fixed, paraffin embedded sections) and spirocysts. Occasional small microbasic-p-mastigophores scattered in epidermis (about  $20\ \mu\text{m}$  long  $\times$   $7\ \mu\text{m}$  in diameter). Cnidoglandular band of mesenterial filaments possesses large microbasic-p-mastigophores (about  $40\ \mu\text{m}$  long  $\times$   $7\ \mu\text{m}$  in diameter), holotrichous isorhizas (about  $45\ \mu\text{m}$  long  $\times$   $15\ \mu\text{m}$  in diameter), and small microbasic mastigophores (?) (about  $11\ \mu\text{m}$  long  $\times$   $5\ \mu\text{m}$  in diameter). The distribution of these nematocysts varies with location on the filament (ECP, unpublished). Histologically distinguished by well-developed longitudinal retractor muscles along the mesogleal pleats. Gastrodermis lining calicoblastic epidermis features large cells with basophilic globules (osmiophilic, non-PAS positive, non-mucin) up to  $4\ \mu\text{m}$  in diameter, which increase in number and density towards base of the polyps. Calicoblastic epidermis thickened with fine eosinophilic granules (Peters 1984). Colonies gonochoric (=dioecious), gametes spawned annually (Szmant-Froelich et al. 1980, St. Pierre 1986).

*Remarks.*—*Madrepora poculata* was described by Ellis & Solander (1786), based on the illustration of a specimen from “near

New York” figured by Ellis (1755). Another reference to this “American” coral appeared in Pallas (1766) under the name *Madrepora calycularis*, var.  $\beta$ . Typical *M. calycularis* Pallas (1766) is now known as *Astroides calycularis* (Pallas, 1766), found only in the Mediterranean (Zibrowius 1980). Therefore, the name *calycularis*, even if applied to a specimen of western Atlantic *Astrangia* as form  $\beta$ , is preoccupied by the Mediterranean species. Esper (1790:283) equated *M. poculata* with the *M. calycularis*  $\beta$  of Pallas, describing a corallum encrusting an American gastropod, which may have been the same as the astrangid-encrusted specimen of *Conus spurius* from the West Indies, figured by Seba (1758:152, pl. 55, figs. 11, 12). The last known reference to *M. poculata* was Turton (1806).

ME & H (1848b) described *Astrangia michelinii* as an illustration found in *Memoire 4, Monographie des Astreides*; this is a valid “indication” (International Code of Zoological Nomenclature (ICZN) 1985: Article 16, vii), and therefore it is a valid species and the type species of *Astrangia* by monotypy. It was described without a type locality.

In 1849, ME & H described (in order) 3 types in the *Muséum National d'Histoire Naturelle*, Paris, (MNHN), *Astrangia danae*, *Astrangia michelini*, and *Astrangia astreiformis*. The descriptions of the type specimens were very similar. They noted that *A. michelini* was closely related to *A. danae*. Unfortunately, only the type locality of one of the 3 species, *A. astreiformis*, was given, as from the “United States.”

Agassiz (1850) described the same species from the United States and used one of the same names used by ME & H, *Astrangia danae*, in a paper presented before the American Association for the Advancement of Science meeting in 1849, but it was not published until 1850. He made no comparisons and apparently did not know that the name had already been used for a species in the previous year (ME & H 1849), and

therefore was a junior primary homonym. It is curious that Dana (1872, 1890) referred to *A. danae* Agassiz, suggesting that he had not been in correspondence with ME & H in the late 1800's. Dana noted that he himself had proposed the name *Pleiadia* for the genus, alluding to the crowd of stars (the appearance of the corallum), in his report on Zoophytes (Dana 1846:722, Wells 1986: 50, nom. nud.). However, Agassiz (1850: 69) made no reference to this particular report. That he chose to call his species *As-trangia* presumably means that he had seen the figure (if not the specimen on one of his European trips) of *A. michelinii* published in 1848.

Later authors, who had compared the type specimens and descriptions, commented on the relations of these species. Vaughan (1901:300) noted that the specimen of *As-trangia astreiformis* (corallites free above their bases), which he had collected in Puerto Rico, was not typical of the specimens of *A. astreiformis* then in the USNM, and observed that the figure of *A. michelini* ME & H "suggests great similarity to the specimen from Puerto Rico." Alloiteau (1952) believed that *A. michelini* ME & H was the same species as *A. danae* Agassiz. Chevalier (1966) observed that *A. astraeiformis* ME & H was similar to *A. michelini* of ME & H. Thus, *A. michelinii* Milne Edwards & Haime is "similar" to *A. danae* Agassiz (Vaughan & Wells 1943, Alloiteau 1952), *A. astreiformis* ME & H (Vaughan 1901, Chevalier 1966), and *A. danae* ME & H (Milne Edwards & Haime 1849).

Leidy (1855) considered *Astrangia astreiformis* ME & H to be the same as *A. danae* Agassiz. In 1863, Verrill recorded that *A. danae* Agassiz was equal to the *A. astreiformis* described by Leidy in 1855, and noted that *A. danae* Agassiz was not the same as *A. danae* ME & H. Verrill (1866a) reported that *A. bella* E. & H. [ME & H], known from the Miocene formations in Maryland, was very similar to both *A. danae* Agassiz and *A. astreiformis* ME & H, and

noted that some authors would unite all three species. Pourtalès (1871:80) remarked "The differences between these two species (*A. astreiformis* M. E. & H. and *A. danae* Ag.) are of the slightest character, being chiefly derived from the mode of grouping, which is denser in the first than in the second. I am strongly inclined to believe that they will ultimately be united." In 1872, Verrill united *A. astreiformis* ME & H with *A. danae* Agassiz. Cummings (1983) and Jaap (in prep.) united *A. astreiformis* ME & H with *A. danae* Agassiz, noting the great variability in specimens collected from throughout its range along the coastline of the eastern United States. Only Vaughan (1901) felt that there were sufficient distinctions based on the skeletal structures to maintain *A. astreiformis* ME & H and *A. danae* Agassiz as separate species.

Thus, these observations link *Astrangia astreiformis* ME & H with *A. danae* Agassiz. Although *A. danae* ME & H appeared to be very similar to *A. astreiformis* ME & H (Leidy 1855, Chevalier 1966) and *A. michelini* ME & H (Milne Edwards & Haime 1849), subsequent authors (Verrill 1863, 1866a) did not connect *A. danae* ME & H with *A. danae* Agassiz. Verrill (1866a:324) stated again that *A. danae* ME & H ("the corallites being scattered and connected only at the base") was different from *A. danae* Agassiz, and therefore proposed the name *A. edwardsii* as a replacement name for *A. danae* ME & H. He erroneously thought that the date for Agassiz's name was 1849 and the date of ME & H's was 1850, because this latter date was cited in error by ME & H (1857:614). A number of later references attributed the publication date of Agassiz's name to 1847 (e.g., Calder 1972) or 1848 (e.g., Field 1949), further adding to the confusion. Fewkes (1889:8) noted that "The polypdom of *A. Danae* (sic) M. E. & H., is held by Prof. Joseph Leidy to be different from that of our New England species of *Astrangia* and more like *A. astraeiformis* of the same authors . . . . It is not possible to determine

from the description of *A. Danae* given by Milne Edwards & Haime whether our species differs from that which they describe under that name or not."

J. W. Wells examined the type specimens in the MNHNP in 1934. Of *Astrangia michelini* ME & H 1848 (No. 412, Michelin Coll.), he noted "Does not look like the figure but has M.E. & H.'s label on the wooden base. Very like *A. danae* [no authority cited] except for smaller [corallites] (2.5–3.0 mm). It is attached to a bit of igneous rock. This is the type species of *Astrangia* by monotypy. No loc." (JWW notes, February, 1934). He also observed that in the Paris collection "Specimens labeled *A. danae* [ME & H 1849] are from St. Thomas and are *A. solitaria*, coll. Duchassaing ca. 1846, except for one that appears to be the type. It encrusts a *Tellina* and fits the description well and is evidently conspecific with *A. michelini* as latter was figured in 1848 by M.E.&H. Has M.E.&H.'s label. No loc." Wells noted that the type of *A. astreiformis* ME & H 1849 was in the Paris collection in 1934, with the locality designated "Etats-Unis," but did not make any other observations on this specimen (JWW notes, February, 1934). From all indications (Cairns 1981), all of the types are now missing from the collections of the MNHNP.

Wells considered *Astrangia danae* ME & H 1849 to be the proper name for the American northern star coral (pers. comm. to A. Szmant-Froelich, 13 December 1977), noting that "Over the years I have examined many specimens from throughout this range [Massachusetts to Texas] and although there is much variation in skeletal morphology, the variation seems not be geographical or provincial, for specimens from one locality frequently show the full range of variation in compactness or isolation of corallites, size of corallites, equality of septa, etc." Although the names *A. danae* Agassiz and *A. astreiformis* ME & H had been used nominally to separate specimens from north of Cape Hatteras to New England from those

specimens collected from south of Cape Hatteras into the eastern and western Gulf of Mexico, respectively, Wells observed that *A. danae* ME & H had priority as the senior synonym.

Cairns (1981) argued that *Astrangia astreiformis* was the appropriate name for the American species. He noted that ME & H described both *A. danae* and *A. astreiformis* in the same paper. Although *danae* had page priority, the type was lost, the description poor, and the type locality not given. He could not confirm that *A. danae* ME & H was the same as *A. danae* Agassiz and *A. astreiformis* ME & H, hence, he considered *A. danae* ME & H to be a nomen dubium. The locality for *A. astreiformis* was given as "United States." Although the type of *A. astreiformis* was also lost, it at least had a type locality, which is why Cairns considered it as the senior synonym. Because Agassiz's description of the same species, which he named *A. danae*, was not published until 1850, Cairns also considered this name a junior synonym of *A. astreiformis* and junior homonym of *A. danae* ME & H 1849.

Based on our present examinations of specimens and recent biological data (see below), we concur that there is only one species of star coral of the genus *Astrangia* along the Atlantic and Gulf coasts of North America. Although the type specimens are now missing from the Michelin collection, earlier observations by Leidy, Verrill, Pourtalès, Fewkes, Wells, Alloiteau, and Chevalier suggest that the *Astrangia* types established by ME & H were very similar. The latter four authors thought that these types were probably only morphological variants of the colonial northern star coral. There is no doubt that this species is the same as the *Madrepora poculata* described by Ellis & Solander over 200 years ago. Although the names *A. danae* and *A. astreiformis* have been used widely in the recent literature (73 and 41 references, respectively), these names must be considered junior subjective syn-

onyms. We conclude that the correct name, based on the Principle of Priority (ICZN 1985), is *Astrangia poculata* (Ellis & Solander, 1786).

The type specimen of *Madrepora poculata* is not present at the Glasgow or the British Museum (Natural History) and is believed to be lost (P. F. S. Cornelius, pers. comm.). In order to help clarify the complex nomenclatural issues concerning the names *Astrangia poculata*, *A. michelinii* ME & H 1848, *A. danae* ME & H 1849, *A. astreiformis* ME & H 1849, and *A. danae* Agassiz 1850, a neotype is chosen for *M. poculata*. It is deposited at the USNM (USNM 80350) and was collected from New Jersey, relatively close to the original type locality of "off New York."

As mentioned before, there is no type specimen of the type species *Astrangia michelinii* (see Chevalier 1966). Furthermore, it was described without a type locality and its original description and figures do not reliably distinguish it from the other approximately 30 Recent species in the genus. Subsequent references to *A. michelinii* have always been in its capacity as the type species of the genus, not as a new record. Therefore, in order to redefine *A. michelinii*, and the genus *Astrangia* by virtue of its status as the type species of the genus, a neotype is chosen for *A. michelinii*. Because several authors (e.g., Vaughan 1901, Alloiteau 1952, Chevalier 1966) have suggested that *A. michelinii* is synonymous with the United States east coast species, the neotype chosen for *A. michelinii* is a specimen of *A. poculata*, in fact the same specimen chosen as the neotype of *M. poculata*, a specimen from New Jersey (USNM 80350). *A. michelinii* thus becomes a junior objective synonym of *A. poculata*.

Thiel (1928) described a colonial *Astrangia* from the Atlantic coast of Africa, and identified it as *A. astreiformis* ME & H. In 1941, Thiel doubted the existence of the American species on the west coast of Africa, and established the species *A. merca-*

*toris* as the African species. Buchanan (1954) reported *A. astreiformis* from the Ivory Coast and Gulf of Guinea off western Africa. Buchanan (1954:86) remarked that his specimens agreed well with Thiel's (1928) description of *A. astreiformis* from Africa. Chevalier (1966), however, believed that the American and African specimens that he examined were sufficiently similar to merit recognition as the same species. Unfortunately, as we know nothing of the African *Astrangia*, Thiel's (1928) specimens may indeed represent a different species.

*Material examined.*—From the USNM, 85 lots, the specimens representing the following localities: Martha's Vineyard Sound, Buzzards Bay, Woods Hole, Massachusetts; Newport, Rhode Island; 19 lots from R/V *Gosnold* collected off northeastern Florida and Georgia (13–54 m); Chesapeake Bay, Virginia Beach, Virginia; Cape Henry, North Carolina; Myrtle Beach, South Carolina; Nassau County, Florida; northeastern coast of Florida; Dry Tortugas, Western Dry Rocks off Sand Key, Florida; Marco, Gulf coast of Florida; Rockport, Galveston, Port Aransas, Texas.

Specimens from the Texas coast deposited in the Texas Memorial Museum, Austin, Texas (Numbers 1568–1573, 1753).

Specimens from the Hourglass Cruises, deposited in the collection of the Department of Natural Resources, Bureau of Marine Research, St. Petersburg, Florida (Numbers FSBC I 10027, 11360, 17984, 19858–19862) and 49 other cataloged specimens (various numbers from FSBC I 10028–31954, eastern Gulf of Mexico and Florida east coast), as well as specimens on loan from Texas A&M University (College Station, Texas), and Museum of Comparative Zoology (Harvard University, Cambridge, Massachusetts), representing locations from New England to Florida, Louisiana, and Texas.

*Geologic and geographic distribution.*—*Astrangia poculata* is recorded from the Miocene (Richards & Harbison 1942),

Pleistocene (Blake 1953, Pampe 1971) and Recent (Alloiteau 1952, Wells 1956). It occurs at depths from 0 to 263 m. It has been reported off Maine (Hargitt 1914) and from Cape Cod south along the eastern United States, around the Gulf coast of Florida to the southern Gulf coast of Texas and Mexico (E. Jordan pers. comm. to WCJ). It is very rare in the coastal region from south of Palm Beach to the Ten Thousand Islands, Florida, and is disjunct in the Mississippi delta region. It is also noted from Puerto Rico (Vaughan 1901) and Martinique (Thiel 1941). Thiel (1928) and Buchanan (1954) reported it from the Ivory Coast, French Congo, Angola, Africa, (although its existence off Africa based on these reports has been questioned, see Remarks), and Chevalier (1966) reported it from the Bight of Biafra, Freetown, Sierra Leone, Konakry, Guinea, Dakar and Senegal (Gulf of Guinea), Africa.

*Discussion.*—Coral species traditionally have been determined on the basis of their skeletal morphologies (since these are preserved most easily, and appear in the fossil record). Veron (1982) stated that biological species in corals are "the sum of a series of forms of variation which differ in relative importance from species to species." Recent attempts to determine the range of variation which may exist within a single species have revealed the relative influence of phenotypic and genotypic variation in skeletal development, and the contributions of each may vary between species or genera (see reviews by Wijsman-Best 1974; Foster 1979, 1980). Lang (1984) reviewed the utility of non-skeletal characters to aid in the differentiation of species when skeletal characters are ambiguous or environmentally variable.

Recent studies have revealed a wide range of variation in the types of skeletal structures produced by colonies of *Astrangia poculata*. Field (1949) reported that branching forms might be found when the colonies were located in a protected spot. Cummings (1983) investigated patterns of morpholog-

ical variability in colonies of *A. poculata* from Rhode Island and the Gulf coast of Florida and found a high degree of morphologic plasticity. She noted that the parameters measured (height/length, branching, and polyp density) were correlated with exposure (light and wave action), and did not differ significantly between zooxanthellate and azooxanthellate colonies. Colonies from Panacea, Florida were, however, more branched than those from Fort Wetherill, Rhode Island, and contained more zooxanthellae per unit area of tissue. The Fort Wetherill colonies possessed more corallites per unit area and were smaller than elsewhere. As depth increased, colonies became taller and more branched, and polyp density decreased. Brunet (1982) described colonies from various sites off the Texas coast. Encrusting, mound and digitate colonies were found at the Port Aransas jetty on the channel at the end of the barrier island. Mostly mounding and a few encrusting colonies, only rarely with early digitate morphologies, were present on the pilings of the near-shore oil rigs he examined. He suggested that the digitate growth form was a response to sedimentation, to allow the polyps to extend above the substratum. He also noted that the appearance of filamentous algae growing on dead portions of the corallum might force adjacent polyps to continue growing and overtop the algae to form characteristic knobby branches. The large expansive polyps of the star coral are well-suited to removing sediment particles that may fall on its surface (Peters 1984). However, we (ECP, CEV, LSG) have observed that during periods of cold weather (in both Rhode Island and Texas corals) the coenosarc tissues of *A. poculata* often contract and expose the coenosteum (as the polyps contract and forego feeding), which may be covered with sediment or colonized by algae. These lesions may contribute to the formation of digitate colonies when the coral resumes skeletal deposition in the spring, although this has not been confirmed ex-

perimentally. St. Pierre (1986) also observed high variability in colony morphology from encrusting to ramose or both types on the same colony, at the Port Aransas jetty. Jaap (in prep.) noted that substratum may also control colony morphology, with encrusting forms found on mollusk fragments or shells and thicker or branching forms on igneous rock bases. As for other skeletal characters, Jaap (in prep.) reported that Gulf of Mexico specimens generally had smaller corallite diameters and there were reduced numbers of septa in specimens taken from Texas or the western Gulf sites. He observed a minimum annual growth rate (basal diameter) of 38.4 to 46.8 mm for two clusters of *Astrangia* which attached to a stone crab trap between April and September 1977 (Jaap, in prep.). The largest branching specimen in the USNM (USNM 78508, Fig. 4) was collected from 263 m depth off Western Dry Rocks, Sand Key, Florida.

The cellular composition and structure of *Astrangia poculata* are distinctive, particularly in the development of the mesogleal pleats and the granules in the cells of the aboral gastrodermis and calicoblast epidermis, and differ from other members of this and closely-related families, such as the Oculinidae (see Peters 1984). *A. poculata* is one of the few subtropical to temperate corals that may possess symbiotic dinoflagellate algae known as zooxanthellae within its gastrodermal tissues, and is the only member of the genus reported to do so. Cummings (1976), Jacques et al. (1977), and Szmant-Froelich (1980a) showed that zooxanthellae densities in some colonies from Narragansett Bay may be equal to or greater than those reported to occur in tropical reef corals. In Narragansett Bay, colonies with zooxanthellae are found directly adjacent to those without, and there are colonies that are only partially pigmented (spotted) brown by the algae. All varieties are found throughout the year. Colonies which appear to lack zooxanthellae usually possess small popu-

lations of the algae (less than  $1 \times 10^5$  cells per polyp). Hence, Swart's (1983:72) arguments that colonies of *A. danae* (= *A. poculata*) that lack zooxanthellae might be a different species, or might be found under stress conditions, appear to be invalid.

Algal populations do vary seasonally with changes in light intensity and temperature (Cummings 1983), and under sedimentation stress (Peters & Pilson 1985). The algal populations also increase under conditions of high light and temperature in the laboratory (Cummings & McCarty 1982, Cummings 1983, Peters & Pilson 1985). Cummings (1976, 1983) suggested that this change was caused by differences in physiological tolerances between zooxanthellate and azooxanthellate colonies, with the former better adapted to summer (high temperature and light) and the latter better adapted to winter (low temperature and light) conditions. Possibly, because of the seasonal fluctuations of these conditions, fully zooxanthellate colonies are not numerically dominant in Narragansett Bay. Jacques (1978) observed that at high light and temperature conditions, the zooxanthellate colonies calcified significantly faster than azooxanthellate ones. Peters & Pilson (1985) found that the tissues of zooxanthellate colonies were more easily damaged by combined sedimentation and starvation stress than azooxanthellate colonies, and suggested that genetic as well as environmental factors influence the symbiosis. Weston (1980) found only zooxanthellate colonies in the relatively well-illuminated surface waters of Chesapeake Bay and azooxanthellate colonies deeper. Both kinds were found inhabiting a transition zone, the depth of which correlated with 89 to 95% attenuation of surface incident light. He also suggested that both genetic and environmental factors might influence the symbiosis. The colonies which Brunet (1982) found on shallow substrata (less than 2 m water depth) at the Port Aransas, Texas, jetty site contained zooxanthellae. At depths greater than

2 m, and at the oil rig and the Liberty ship, specimens of *Astrangia* always lacked zooxanthellae.

Colonies of *Astrangia poculata* tolerate a wide variety of environmental conditions. In nature, populations have been found in salinities ranging from oceanic (36‰) seawater (Cummings 1976) to salinities of 16–19‰ in Texas bays (Ladd 1951). Experimentally, this coral can adapt to salinities ranging from 10 to 40‰ (Ferguson 1948, Cummings 1976) and can survive for more than six days under low oxygen conditions (Sassaman & Mangum 1973). In Narragansett Bay, Rhode Island, *A. poculata* survives an annual temperature range of  $-1.5^{\circ}\text{C}$  to  $22^{\circ}\text{C}$ , and up to  $35^{\circ}\text{C}$  under experimental conditions in the laboratory (Cummings 1976, Jacques 1978, Peters & Pilson 1985). St. Pierre (1986) observed annual temperature fluctuations from  $17^{\circ}\text{C}$  to  $30^{\circ}\text{C}$  during a study of *Astrangia* from Port Aransas, Texas. The unusual hardiness of *A. poculata* is illustrated by the fact that MEQP (unpublished) often kept colonies in small containers in his office. In one case a small colony was maintained for more than three years in a one-liter container, often without feeding it or changing the water for months.

The sexual reproduction of *A. poculata* in Narragansett Bay, Rhode Island, was examined by Szmant-Froelich et al. (1980). They demonstrated that each colony is dioecious, with a 1:1 male:female sex ratio for the population. Fertilization is external, with development of planktonic planula larvae, and zooxanthellae are not passed on in the eggs or sperm but must be acquired after settlement. An annual reproductive cycle appeared to be tied to the seasonal maximum temperature. Well-fed colonies, experimentally maintained year-round under high light and temperature ( $20$ – $22^{\circ}\text{C}$  or  $26^{\circ}\text{C}$ ) conditions continuously produced gametes (Szmant-Froelich 1981, Peters & Pilson 1985). St. Pierre (1986) studied the reproductive cycle of a population of *Astrangia* from a jetty off Port Aransas, Texas. She

also found a 1:1 sex ratio. Gametogenesis began in February, with spawning occurring in late August to September, corresponding to the maximum water temperatures at this Gulf of Mexico site. Another cycle of gametogenesis appeared to begin in November. Similarly, a second cycle was reported for the Rhode Island colonies beginning in October. Because the reproductive cycle of this coral appears to be essentially the same throughout its range, St. Pierre supported the synonymy of *A. danae* with *A. astreiformis* (St. Pierre 1986).

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