SIGNIFICANCE OF COILED PROTOCORALLA IN SOME MISSISSIPPIAN HORN CORALS

by WILLIAM J. SANDO

ABSTRACT. Planispirally coiled protocoralla are described in *Cyathaxonia tantilla* (Miller) from the Lower Mississippian (Lower Carboniferous) of the western United States, the first record of this phenomenon in corals. Coiling is interpreted as a mode of attachment of young coralla to planktonic algae. The postulated pseudoplanktonic growth habit may be a significant factor in the widespread distribution of this species and other species of *Cyathaxonia*, which are generally found in rocks that record a bottom environment considered unfavourable for optimum coral growth.

SPECIMENS of horn corals with perfectly preserved tips are rarely observed in compact Palaeozoic limestones, even though corals are abundant in these rocks. Freeing of silicified specimens from limestone matrix by dissolving the matrix in acid often provides unusual opportunities to observe the earliest growth stages of these corals. This report presents the results of a study of approximately 500 etched silicified specimens of *Cyathaxonia tantilla* (Miller) from the Paine Member of the Lodgepole Limestone (Lower Mississippian, Kinderhookian, lower Tournaisian) collected from seven localities in the western United States (Utah and Montana). At Brazer Canyon, Utah, samples collected from closely spaced intervals through the lower part of the Lodgepole Limestone provided an unusual opportunity to study morphological variation in the earliest stage of these small horn corals. The Brazer Canyon material revealed a planispirally coiled protocorallum never before reported in corals. Discovery of the same phenomenon in specimens from four other localities suggests that a coiled brephic stage was a common feature of *C. tantilla*.

NATURE AND SIGNIFICANCE OF THE BREPHIC STAGE

Nature of samples. The material from Brazer Canyon was collected from 0·3 m intervals through the lower 14·4 m of the Lodgepole Limestone and from 15·6 m and 18·7 m above the base. Three hundred and twenty specimens of *C. tantilla* in which all or part of the brephic stage (0–6 septa) is preserved were isolated for analysis from the Brazer Canyon samples (Table 1). In the overwhelming majority of these specimens (288), no evidence of attachment was observed. In most specimens, the tip was broken off (Pl. 12, fig. 7); in some, the tip is preserved, but abraded (Pl. 12, fig. 4). Perfect specimens are in two categories: (1) coiled tip (25 specimens) (Pl. 12, figs. 11–18), and (2) tip with lateral or basal attachment scar (7 specimens) (Pl. 12, figs. 9, 10). Coiled tips are present throughout almost the full stratigraphic range of the species (Table 1). Perfect tips are similarly rare in samples of *C. tantilla* from other localities in Montana and Utah (Table 2). Thus, out of approximately 500 specimens studied, all or part of the brephic stage is preserved in 348, but

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breakage or abrasion of the tip prevents determination of the nature of attachment in all but 38 specimens, of which 30 have coiled tips and 8 have lateral or basal scars of attachment.

TABLE 1. Nature of protocorallum in 320 specimens of *Cyathaxonia tantilla* (Miller) from Brazer Canyon section, Utah.

Number of specimens with preserved brephic stage

Metres above base of Lodgepole Limestone	USGS Upper Palaeozoic locality number	Coiled tips	No evidence of attachment	To	
0-0.6	16801-PC, 16802-PC	8	- 3	59	
0.6 - 1.2	16803-PC, 16804-PC	9	2	119	1
1.2-1.8	16805-PC	2	0	18	
1.8-2.4	16806-PC, 16807-PC	0	0	0	
2.4-3.0	16808-PC, 16809-PC	1	0	11	
3.0-3.6	16810-PC	0	0	2	
3.6-4.2	16811-PC	· 1	0	2	
4.2-4.8	16812-PC	0	0	1	
4.8-5.4	16813-PC	0	0	2	
5.4-6.0	16814-PC	0	0	0	
6.0-6.6	16815-PC	0	0	5	
6.6-7.2	16816-PC	1	0	1	
7.2-7.8	16817-PC	0	0	1	
7.8-8.4	16818-PC	0	0	5	
8.4-9.0	16819-PC	0	0	0	
9.0-9.6	16820-PC	0	0	3	
9.6-10.2	16821-PC, 16822-PC	0	0	3	
10.2-10.8	16823-PC, 16824-PC	0	0	1	
10.8-11.4	16825-PC	0	1	4	
11.4-12.0	16826-PC	1	0	3	
12.0-12.6	16827-PC	0	1	27	
12.6-13.2	16828-PC	2	0	14	
13.2-13.8	16829-PC	0	0	6	
13.8-14.4	16830-PC	0	0	0	
15.6	16831-PC	0	0	1	
18.7	16832-PC	0	0	0	
	Totals	25	7	288	3

TABLE 2. Nature of protocorallum in specimens of *Cyathaxonia tantilla* (Miller) from localities in Montana and Utah other than Brazer Canyon.

Number of specimens with preserved brephic stage **USGS** Upper Lateral No evidence Palaeozoic Total attachment of attachment Locality locality number Coiled tips 2 Logan, Montana 17356-PC 0 0 0 4 4 17357-PC 0 5 6 White Peak, Montana 20164-PC 1 2 0 3 Squaw Creek, Montana 1 20600-PC 7 9 2 0 Sacajawea Peak, Montana 20641-PC 0 1 0 1 Emma Canyon, Utah 16911-PC 2 0 1 Baldy Mountain, Montana 17911-PC 1 0 0 0 0 17913-PC 0 0 0 17914-PC 0 0 0 1 1 17915-PC 5 22 28 Totals 1

Description of coiled tips. The brephic stage (protocorallum) is defined as the part of the corallum in which the first six septa (protosepta) appear. It is distinguished externally by the absence of the longitudinal septal grooves and interseptal ridges present in later growth stages (Pl. 12, figs. 12, 13). In the thirty specimens with coiled tips, the protocorallum ranges from 0·9 to 2·0 mm in length and has a mean length of 1·3 mm. In the lower half of the protocorallum, the corallum is evolutely coiled, ordinarily planispirally, to form a single 360° volution. The diameter of the coil ranges from 0·5 to 1·0 mm and has a mean value of 0·7 mm. The diameter of the corallum at the top of the volution ranges from 0·4 to 1·0 mm and has a mean value of 0·6 mm. The corallum is coiled about an open umbilicus which ranges from 0·05 to 0·30 mm in diameter and has a mean diameter of 0·13 mm.

Above the coil, the protocorallum may be erect (no change in direction of the corallum axis), geniculate (one or more changes in direction of the corallum axis in one plane), or vermiform (one or more changes in direction of the corallum axis in more than one plane). In the specimens studied, 47% are erect, 23% are geniculate, and 30% are vermiform. One or more protosepta were observed within the coiled part of the corallum in seven specimens.

Coiled tips are ordinarily observed in individuals that died in the neanic stage. The length of the corallum in specimens studied ranges from 1·9 to 14·2 mm, but the mean length is only 4·2 mm, and all but two specimens are 6·5 mm long or less. The maximum corallum diameter in these specimens ranges from 1·2 to 4·5 mm, but the mean diameter is 2·4 mm, and all but two specimens have a maximum diameter of 3·5 mm or less. The number of septa in the calice ranges from 6 to 34, but the mean is 22, and all but one specimen has 30 septa or less.

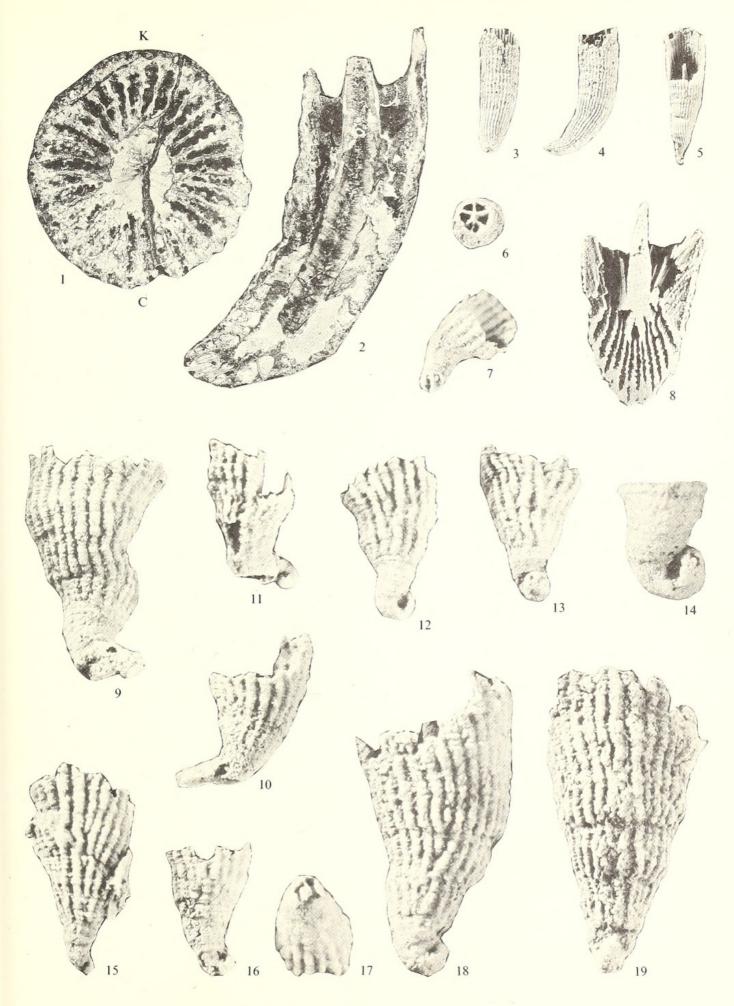
Interpretation. Most small, solitary, curved-conical rugose corals observed by the writer show basal or lateral attachment scars in young specimens in which the protocorallum is preserved, indicating that these corals ordinarily were fixed to some stable object on the substrate immediately after settling of the larvae. Attachment scars are not ordinarily seen on adult specimens of these corals; this suggests that the corallum subsequently broke loose from its attachment when its weight became too great for the cemented tip to support, and then lay on its side, changing its growth direction in order to maintain a position conducive to optimum feeding and growth. Evidence and theories bearing on the growth habits of such corals have been summarized by Sando (1961, pp. 75-79). Lateral or basal attachment scars were observed in 8 of the 38 specimens of C. tantilla having perfectly preserved tips, indicating that some of these corals followed the common growth pattern. The presence of a coiled tip and the lack of attachment scars in the other thirty specimens suggests that coiling about some linear object was the principal mode of fixation of the protocorallum. In order to coil about an object lying on the substrate, the polyp would have had to exert a lifting force or to submerge its feeding mechanism in the substrate; the object of attachment was therefore probably above the substrate. The only linear objects of diameter comparable with that of the umbilicus of the coiled tip found in the coral samples are productoid brachiopod spines (0·1-0.2 mm diameter) and the crossbars in fenestellid bryozoan zoaria (0.1-0.2 mm diameter). These are rejected as objects of attachment because none of the coralla were

found attached to them and because many of the coralla have an umbilicus of smaller diameter (0.05 mm) than the diameter of the postulated attachment objects.

The absence of attachment objects within the umbilici of the coiled tips suggests that the objects were composed of material that was not preserved. The filaments of modern marine algae are in the size range required (W. H. Adey, pers. comm. 1975), and marine algae are widely known from rocks of Mississippian age. However, the only possible algal remains known from the Paine Member of the Lodgepole Limestone are forms identified as Calcisphaera, Vicinisphaera, Bisphaera, and 'Radiosphaera' (Mamet in Sando et al. 1969, p. E-13), which are thought to be planktonic algal cysts (B. L. Mamet, pers. comm. 1975). The associated benthonic fauna of foraminifers, corals, brachiopods, gastropods, bryozoans, and pelmatozoans consists of sparse, poorly diversified and depauperate forms adapted to an impoverished environment. The dark, thin-bedded, cherty, fine-grained, argillaceous, and silty beds of the Paine Member have been interpreted as sediments deposited in relatively deep, turbid water (Wilson 1969, pp. 15-16; Smith 1972, p. 31; Sando 1976), and as much as 50 m of relief has been measured on associated bioherms (Cotter 1965, p. 888). Thus, the weight of evidence favours an aphotic bottom environment for the Paine Member, which would preclude attachment of Cyathaxonia tantilla to benthonic algae.

EXPLANATION OF PLATE 12

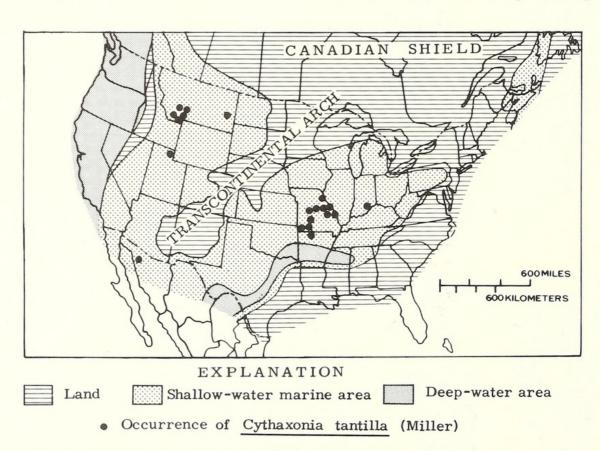
- All specimens are *Cyathaxonia tantilla* (Miller) from the Paine Member of the Lodgepole Limestone. All but fig. 5 are from Brazer Canyon, Utah.
- Fig. 1. Transverse thin section, ephebic stage, USNM 222532b, USGS loc. 16803-PC, ×12.
- Fig. 2. Longitudinal thin section, ephebic stage, USNM 222530, USGS loc. 16803-PC, ×7.
- Figs. 3, 4. Counter and alar views, respectively, of etched ephebic corallum having abraded tip, USNM 222529, USGS loc. 16803-PC, ×2.
- Fig. 5. Alar view, etched ephebic corallum having coiled tip, USNM 222591, USGS loc. 20641-PC, Sacajawea Peak, Montana, ×2.
- Fig. 6. Broken tip of etched brephic corallum showing 6 protosepta, USNM 222544, USGS loc. 16803-PC, ×10.
- Fig. 7. Broken tip of etched brephic corallum showing initial axial septum, USNM 222520, USGS loc. 16801-PC, $\times 10$.
- Fig. 8. Broken etched ephebic corallum showing tuberculated septa, USNM 222545, USGS loc. 16804-PC, × 5.
- Figs. 9, 10. Alar views of etched neanic coralla showing lateral and basal attachment scars. 9, USNM 222524, USGS loc. 16802-PC, ×10. 10, USNM 222518, USGS loc. 16801-PC, ×10.
- Fig. 11. Alar view of etched neanic corallum having coiled tip, USNM 222516, USGS loc. 16801-PC, × 10. Figs. 12, 13. Alar and cardinal views, respectively, of etched neanic corallum having coiled tip, USNM 222514, USGS loc. 16801-PC, × 10.
- Fig. 14. Enlarged alar view of protocorallum of specimen shown in figs. 12 and 13, USNM 222514, USGS loc. 16801-PC, ×20.
- Fig. 15. Cardinal view of etched neanic corallum having coiled tip, USNM 222517, USGS loc. 16801-PC, × 10.
- Figs. 16, 17. Alar and tip views, respectively, of etched neanic corallum having broken coiled tip showing axial septum, USNM 222536, USGS loc. 16803-PC, ×10.
- Figs. 18, 19. Alar and cardinal views, respectively, of etched neanic corallum having coiled tip, USNM 222515, USGS loc. 16801-PC, ×10.



SANDO, Mississippian corals

The corals were probably attached to algae that were floating in the photic zone of the sea-water. The small size and consequent low mass of the young corallum is compatible with a planktonic habit. Prior to maturity, increased mass of the corallum may have caused most individuals to descend to the sea-floor, where they spent the remainder of their lives lying on their sides. These forms produced a curved corallum in response to the need for maintaining their oral surfaces in an optimum feeding position (Pl. 12, fig. 14). Ordinarily the delicate coiled protocorallum was destroyed on the sea-floor either by other organisms (see Sando 1961, p. 79) or by mechanical abrasion while the corallum was still occupied by the living polyp or after death. Some individuals (Pl. 12, fig. 5) either survived such destructive influences or remained attached to floating aggregates of algae throughout growth. The straight-conical rather than curved-conical form of the few mature specimens that show coiled tips suggests a pseudoplanktonic habit throughout growth for these individuals. Other individuals having basal or lateral attachment scars evidently were attached to objects on the substrate and were sessile throughout post-larval growth.

Significance. The postulated pseudoplanktonic growth habit of the specimens studied has an important bearing on the migration potential of *Cyathaxonia*. Inasmuch as specimens with perfectly preserved tips are extremely rare, this growth habit may have been a common feature of *C. tantilla* and perhaps other species of the genus. *C. tantilla* occurs in strata of middle and late Kinderhookian and earliest Osagean age in both the western and eastern United States (text-fig. 1) despite a



TEXT-FIG. 1. Palaeogeographical map of the United States and adjacent areas during Kinderhookian time, showing occurrences of *Cyathaxonia tantilla* (Miller).

bottom environment unfavourable to optimum coral growth and the presence of the Transcontinental Arch which acted as a barrier between the two areas.

Meagre data on the migration time of modern coral larvae suggests that most larvae become attached during the first 2 days of their existence, although some remain swimming for as long as 2 months (Connell 1973, p. 209). A pseudoplanktonic brephic-neanic growth habit would increase the time interval available for migration and thus provide a better explanation of the distribution pattern of *C. tantilla*. Species of *Cyathaxonia* have a long stratigraphical range and world-wide distribution despite their almost universal occurrence in dark, silty, argillaceous limestone and calcareous shale, lithofacies that reflect bottom conditions generally unfavourable to the growth of corals. The prevalence of this association prompted Hill (1938, pp. 5–9) to name the biofacies '*Cyathaxonia* Fauna'. A pseudoplanktonic growth habit in other species of *Cyathaxonia* might be a factor in the widespread distribution of the genus.

SYSTEMATIC PALAEONTOLOGY

Morphological terminology generally follows Hill (1935, 1956). The following abbreviations are used in the text: U.S. National Museum of Natural History, Washington, D.C., U.S.A. (USNM); U.S. Geological Survey, Washington, D.C., U.S.A. (USGS).

Family METRIOPHYLLIDAE Hill, 1939, emend. Rozkowska, 1969 Subfamily CYATHAXONIINAE Milne-Edwards and Haime, 1850 Genus CYATHAXONIA Michelin, 1847

1847 Cyathaxonia Michelin, p. 257.

1928 Cyathocarinia Soshkina, p. 376.

Type species. Cyathaxonia cornu Michelin, 1847, by subsequent designation of Milne-Edwards and Haime 1850. Lower Carboniferous (Tournaisian), Tournai, Belgium.

Diagnosis. Corallum small, ceratoid-cylindrical. Long, contratingent minor septa inserted alternately with metasepta according to metriophyllid septal plan. Columella tall, developed independently of major septa but in contact with them (pseudoseptal columella of Schouppé and Stacul 1961). Tabulae inclined downward towards epitheca. Dissepiments absent. Sides of septa may have rows of tubercles steeply inclined from the horizontal.

Discussion. Corals similar in most morphological aspects to the type species of Cyathaxonia have been found in strata ranging in age from Late Devonian (early Famennian) into Early Permian. Such morphologic similarity has resulted in recognition of the type species throughout the entire stratigraphic range of the genus, although subspecies and other species have been proposed for variations in the size and shape of the columella, septal number, size of the corallum, and length of the minor septa. Modifications of the septa have been variously called carinae, tubercles, or spines. Descriptions and illustrations of these modifications indicate that they consist of rows of rounded or pointed protuberances on the sides of the septa and not continuous ridges or flanges. Smith (1931, p. 8) pointed out that these are not true carinae.

Differences of opinion about the taxonomic significance of tuberculate v. nontuberculate septa have resulted in different generic concepts. Carruthers (1913, p. 56) noted tubercles in the type species and in C. rushiana Vaughan from the Viséan, but did not find them in topotype specimens of the type species (Tournaisian) and did not consider the tubercles of diagnostic value. Schindewolf (1951, p. 99) found tuberculate septa in specimens of the type species from the Tournaisian of France and Viséan of Ireland but not in topotypes of C. rushiana (Viséan). He also noted all variations between forms having smooth septa and forms having well-developed tubercles and concluded that the presence or absence of tubercles has no taxonomic or chronologic significance. On the other hand, Soshkina (1928, p. 376) proposed the subgenus Cyathocarinia for Permian species of Cyathaxonia having tuberculate septa. Some subsequent authors (Soshkina et al. 1941, p. 41; Wang 1950, p. 205; Lecompte 1952, p. 482; Rozkowska 1969, p. 55) have continued to recognize Cyathocarinia as a subgenus of Cyathaxonia, whereas others (Soshkina 1939, p. 51; Kostic-Podgorska 1955, p. 170; Hill 1956, p. 264; Soshkina et al. 1962, p. 333; Ivanovskiy 1967, p. 23) regarded Cyathocarinia as a distinct genus.

Extensive published records of *Cyathaxonia* indicate that both tuberculate and nontuberculate forms are present throughout the long stratigraphic range of the genus. Much variation has been noted in the strength and abundance of the tubercles in forms that are very similar or identical in other respects. In the Mississippian species described herein from the United States, tubercles are not present in the higher parts of the calice or in the earlier parts of the corallum, making recognition difficult in many specimens without serial sectioning. Available data on North American Mississippian species suggest that the presence or absence of tubercles is one of the morphologic characters useful for discrimination of species. However, use of this character for generic or subgeneric discrimination does not result in taxonomic groups that are meaningful phylogenetically. Accordingly, I include both tuberculate and nontuberculate forms in *Cyathaxonia* and regard *Cyathocarinia* as a junior synonym.

Cyathaxonia tantilla (Miller)

Plate 12, figs. 1-18

- 1891 Zaphrentis tantilla Miller, p. 11, pl. 1, figs. 23, 24; Miller 1892, p. 621, pl. 1, figs. 23, 24; Keyes 1894, p. 111; [not] Girty 1903, p. 269.
- 1909 *Cyathaxonia tantilla* (Miller), Weller, p. 270; Grove 1935, p. 367, pl. 9, figs. 15–17; Easton 1944, p. 30, pl. 6, figs. 7, 8; pl. 16, figs. 16, 17; Conkin and Conkin 1954, p. 214, fig. 1A–D.
- 1960 Cyathocarinia tantilla (Miller), Sando, p. 168.
- 1909 *Cyathaxonia minor* Weller, p. 270, pl. 10, figs. 14–17; [?] Girty 1926, p. 24; [not] Davis 1956, p. 29, pl. 4, fig. 3.
- 1960 Cyathaxonia arcuata Weller?, Sando, p. 168, pl. 16, figs. 25-27.
- 1958 Cyathaxonia cordillerensis Easton, p. 13, pl. 1, figs. 14, 17, 18.

Distribution. Chouteau Limestone (Missouri), Fern Glen Limestone (Missouri, Illinois), Springville Shale (Illinois), Hannibal Shale (Illinois), Compton Limestone (Missouri), Sedalia Limestone (Missouri), St. Joe Limestone Member of Boone Formation (Missouri, Arkansas), Reeds Spring Limestone (Missouri), Shale below Rockford Limestone (Indiana), [?] limestone of Boone age (Texas), Paine Member of Lodgepole Limestone (Montana, Utah), Represo Formation (Sonora).

Diagnosis. Cyathaxonia having 28–36 (ordinarily 32) septa in ephebic stage. Corallum attaining a maximum length of about 20 mm and a maximum diameter of about 4.5 mm. Septa tuberculate in late neanic and ephebic stages.

Description of Utah and Montana specimens. Corallum ceratoid in brephic and neanic stages to cylindrical in ephebic stage (Pl. 12, figs. 3-5); cardinal side convex; commonly geniculate, vermiform, or planispirally coiled in brephic stage (Pl. 12, figs. 9-18); attaining a maximum length of 17 mm and a maximum diameter of 4·8 mm. Epitheca marked by strong longitudinal septal grooves and interseptal ridges, transverse rugae, and fine transverse striations (Pl. 12, figs. 3, 4, 9, 14) except in brephic stage, where only transverse striations are present (Pl. 12, figs. 12, 13). Calice as much as 6 mm deep at maturity. Septa number 32-36 at maturity (corallum diameter 4·5-4·8 mm).

Ephebic septal plan (Pl. 12, fig. 1) characteristic of the genus, consisting of cardinal septum in poorly defined fossula bounded by minor septa, major septa that reach columella but do not participate in its formation, counter septum on concave side of corallum, and minor septa that are contratingent on cardinal side of all major septa and fall slightly short of columella. Sides of septa usually have rows of tubercles that slope downward at an angle of 60°-80° from horizontal towards corallum axis (Pl. 12, fig. 8); tubercles present only in late neanic and ephebic stages (below floor of calice and immediately above floor of calice); septa ordinarily smooth in other parts of corallum but may have low ridges corresponding to rows of tubercles in calice. Columella smooth sided; ovate in cross-section with long diameter in cardinal-counter plane; 0·3-0·8 mm in short diameter and 0·9-1·5 mm in long diameter at base of mature calice; tapering to a blade-like point just below top of calice (Pl. 12, figs. 5, 8). Tabulae (Pl. 12, fig. 2) about 0·05 mm thick, concave upward, sloping upward from theca to columella; about five tabulae in vertical distance of 2 mm; not ordinarily seen in etched specimens.

Ontogeny. The earliest growth phase observed (Pl. 12, figs. 7, 16) is in the broken tip of several etched specimens (corallum diameter 0.4 mm), which have a single axial septum, to be differentiated later into cardinal and counter septa. In the next observed growth phase (Pl. 12, fig. 6), 6 protosepta (cardinal, counter, 2 alar, 2 counter lateral) are present at a corallum diameter of 0.7 mm. Development up to and including formation of the 6 protosepta is included in the brephic growth stage, which occupies the first 2 mm of corallum length to a corallum diameter of about 1 mm. The exterior of the corallum is without longitudinal ribbing in the brephic stage. The neanic stage is recognized for the part of the corallum that includes a complement of 7-31 septa to a corallum diameter of about 4 mm. During this stage, the corallum is characterized by maximum curvature and rapid expansion of its diameter. Formation of the columella as a discrete structure is initiated and continues into maturity. Rapid insertion of major and minor septa takes place according to the 'cyathaxoniid' septal plan described by Faurot (1909, pp. 75-80), Duerden (1906, p. 236, figs. 9-12), and Hill (1940, p. 194). In the ephebic stage, the corallum is essentially cylindrical and straight, showing very little expansion in diameter (to a maximum of 4.8 mm) and the insertion of few septa (maximum 32-36).

Discussion. North American species of Cyathaxonia have been differentiated mainly on the maximum size of the corallum, the maximum number of septa, the presence or absence of tubercles on the septa, and, to a lesser extent, on external ornamentation. Although statistical analysis of larger samples may ultimately prove otherwise, available evidence does not support separation of the Utah and Montana samples from samples of C. tantilla from the Mississippi Valley area. Easton (1944, p. 30) found only 28 septa at a corallum diameter of 3.5 mm in the 'most advanced stage observed' in the cotype lot, but Miller (1891, p. 12) recorded a septal number of

30 at a diameter larger than 3 mm in a cotype, Keyes (1894, p. 111) recorded a range of 20–32 septa in specimens from Missouri, and Conkin and Conkin (1954, p. 214) stated that the largest topotype specimens studied by them 'constantly have 32 septa' at corallum diameters of as much as 3·6 mm. The Utah and Montana specimens show a range of 30–36 septa at corallum diameters ranging from 3·5 to 4·8 mm in the largest coralla observed, but almost all the larger specimens have only 32 septa and a maximum diameter ranging from 3·5 to 4·5 mm (one specimen has 36 septa and one specimen has 34 septa).

C. minor Weller (1909, p. 270) is within the range of measurable characters of C. tantilla, as noted by Grove (1935, p. 368) and affirmed by Easton (1944, p. 30). C. cordillerensis Easton (1958, p. 13), characterized by 32–35 septa and a maximum corallum diameter of 4 mm, also cannot be separated from C. tantilla. Sando (1960, p. 168) incorrectly referred specimens of C. tantilla questionably to C. arcuata Weller. A summary of the distinguishing characteristics of the described North American species of Cyathaxonia (Table 3) indicates that C. tantilla differs from all others in having tuberculate septa. Most of the other species have a considerably larger corallum than C. tantilla, with the exception of C. venusta, distinguished by its cuneate corallum, and C. winchelli, a poorly known form that may be a synonym of C. tantilla.

Material studied. USNM 222513-222598. See list of localities for geographic locations and stratigraphic positions of collections.

TABLE 3. Summary of North American species of Cyathaxonia.

Species	Formation	Locality	Maximum septal number	Maximum length (mm)	Maximum diameter (mm)	Other distinguishing features
C. tantilla (Miller, 1891)	See text	See text	36	c. 20	c. 4·5	Tuberculate septa
C. arcuata Weller, 1909	Fern Glen Ls.	Missouri	36	36	7	
C. winchelli Rowley, 1900	Lower Burlington Ls.	,,	36	16?	5?	
C. cynodon (Rafinesque and						
Clifford, 1820)	New Providence Sh.	Kentucky	36	25	7	Epithecal spines
C. bordeni Greene, 1900	,, ,, ,,	Indiana	36	25	8	
C. parva Greene, 1900	" " "	***	50	30	10	
C. venusta Greene, 1904	Salem Ls.	,,	34	15	5	Cuneate corallum
C.? iovaensis Worthern, 1890	Ste. Genevieve Ls.	Iowa	c. 30	32	13	

LIST OF LOCALITIES

- 1. Brazer Canyon section, NW. 4SE. 4Sec. 20, T. 11 N., R. 8E., Rich County, Utah (see Sando *et al.* 1959, fig. 2 for geologic map). Paine Member of Lodgepole Limestone, lower 18.7 m. (USGS locs. 16801-PC-16832-PC) (see Table 1 for exact positions of individual samples).
- 2. Emma Canyon section, NE. ¹/₄SE. ¹/₄Sec. 17, T. 11 N., R. 8 E., Rich County, Utah (see Sando *et al.* 1959, fig. 2 for geologic map). Paine Member of Lodgepole Limestone, 1·8–2·2 m above base (USGS loc. 16911-PC).
- 3. Sacajawea Peak section, south wall of cirque in NE.¼NW.¼ Sec. 27, T. 2 N., R. 6 E., Gallatin County, Montana. Paine Member of Lodgepole Limestone, 6.5 m above base (USGS loc. 20641-PC).
- 4. Logan section, SE.\(\frac{1}{4}\)SW.\(\frac{1}{4}\)Sec. 25, T. 2 N., R. 2 E., Gallatin County, Montana (see Sando and Dutro 1974, pp. 4–8 for geologic map and section description). Paine Member of Lodgepole Limestone, lower 1.5 m (USGS loc. 17356-PC), 3 m above base (USGS loc. 17357-PC).
- 5. Baldy Mountain section, SE.¹/₄NW.¹/₄ Sec. 27, T. 7 S., R. 3 W., Madison County, Montana. Paine Member of Lodgepole Limestone, 0·8–1·4 m above base (USGS loc. 17911-PC), 6·2–7·7 m above base

- (USGS loc. 17913-PC), 9·2-10·7 m above base (USGS loc. 17914-PC), 11·6-15·2 m above base (USGS loc. 17915-PC).
- 6. White Peak section, NE.\(\frac{1}{4}\) Sec. 2, T. 11 S., R. 4 E., Gallatin County, Montana (see Witkind 1969, pp. 89-93 for section description). Paine Member of Lodgepole Limestone, 6\(\cdot 3\)-17\(\cdot 1\) m above base (USGS loc. 20164-PC).
- 7. Squaw Creek section, SE.¹/₄NE.¹/₄ Sec. 34, T. 4 S., R. 4 E., Gallatin County, Montana. Paine Member of Lodgepole Limestone, 2·1-2·6 m above base (USGS loc. 20600-PC).

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