

JERZY FEDOROWSKI and WILLIAM J. SANDO

MORPHOGENESIS AND RELATIONSHIPS OF *TROCHOPHYLLUM*
MILNE-EDWARDS AND HAIME, 1850 (COELENTERATA, ANTHOZOA)

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Detailed study of the holotype and topotypes of the type species of *Trochophyllum* Milne-Edwards and Haime reveals that this genus has a unique internal morphology most similar to *Neaxon* Kullman. Although the systematic relationships of small, aulate solitary corals remain dubious, *Trochophyllum* is referred provisionally to the family Petraliidae de Koninck. The genus is represented by the type species, *T. verneuillanum* Milne-Edwards and Haime, and the informal taxon *T. sp. 1*, which are known only from Tournaisian (early Osagean) strata in Kentucky and Indiana, USA. Previously published records of *Trochophyllum* outside the type locality of its type species are either invalid or unconfirmable on present published information. *Trochophyllum* is distinguished by a highly variable aulos that is typically of the stereotheca-type, filled with stereoplasm at maturity; axial tabulae absent or not preserved at maturity; cardinal septum shortened in the calice; and minor septa developed only as foundations.

Key words: corals, Rugosa, Carboniferous, systematics.

Jerzy Fedorowski: Katedra Geologii, Uniwersytet im. A. Mickiewicza, ul. Mielżyńskiego 27/29, 61-715 Poznań, Poland. William J. Sando: U.S. Geological Survey, E-501 U.S. National Museum of Natural History, Washington, D.C. 20380 USA. Received: May 1988.

INTRODUCTION

Trochophyllum is a genus whose type species, *T. verneuillanum* Milne-Edwards and Haime, is comprised of small solitary corals known only from a narrow stratigraphic interval of Tournaisian (early Osagean) age in the New Providence Shale Member of the Borden Formation in north-central Kentucky and southern Indiana, USA. The holotype of *T. verneuillanum* has not been studied since Milne-Edwards and Haime (1850, 1851) originally described the external features of the genus based on this single specimen collected by Verneuil from the classic Buttonmold Knob locality near Louisville, Kentucky. No other primary type material is known to exist. Stumm's (1948: pl. 17: 25—29) description and illustra-

tions of transverse and longitudinal thin sections of a topotype and Pickett's (1967: pl. 1: 12) discussion and illustration of a transverse thin section of another topotype are the only means of presently evaluating the internal morphology of *Trochophyllum*. The paucity of detailed information on morphological features needed for a modern appraisal of the systematic affinities of the genus, has led to disagreements between coral specialists concerning the relationships of this rare coral to other similar genera such as *Permia* Stuckenbergh of Hudson and *Crassiphyllum* Grove (see Pickett 1967: 7). The few species, exclusive of the type, assigned to *Trochophyllum* from Carboniferous rocks outside of the type area, actually belong to other genera or need further study to determine their true affinities.

The senior author became interested in *Trochophyllum* during an investigation of small aulate solitary corals from the Carboniferous of Spain and solicited the help of the junior author to compile information on this peculiar coral. Because *Trochophyllum* is a part of the North American Midcontinent (Southeastern Province) coral fauna, its systematic relationships have an important bearing on the question of endemism of that fauna (see Sando *et al.* 1977). This paper presents the results of a detailed joint study of the holotype and topotypes of the type species and provides our opinions concerning the systematic relationships and morphogenesis of the genus.

All figures in the text were drawn by the senior author, except where noted.

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MATERIAL STUDIED AND OCCURRENCE

One hundred twenty-three specimens from the type locality and nearby localities from which *Trochophyllum verneuillanum* was reported were available to supplement our study of the holotype. All specimens are at least partly silicified and have their external surfaces completely or partly free of sedimentary matrix. No tips are complete, but several corallites have early growth stages preserved. Calices are commonly flattened and/or lack upper edges. A few specimens are sufficiently well preserved to determine the basic morphology and individual variation of the population.

The specimens were collected randomly from float from the New

Providence Shale Member of the Borden Formation at several localities in the vicinity of Louisville, Kentucky, USA. The New Providence Shale Member is of Tournaisian (early Osagean) age and represents the pro-deltaic phase of the Borden delta in Indiana and northern Kentucky (Ausich *et al.* 1977; Kramer 1985). The corals are restricted to aerobic-zone clay shale in the lower 55 m of the New Providence Member, above a basal 6 m-interval of dysaerobic basinal shale (Kammer 1985, and oral commun. 1985). The original life-zone of the corals is estimated by Kammer (oral commun. 1985) as 100–150 m below sea level. One hundred seven of the specimens studied are referred to *Trochophyllum verneuilanum* Milne-Edwards and Haime, but 16 that have an empty aulos are separately designated *Trochophyllum* sp. 1, which is not given formal status because of the absence of data on exact stratigraphic relations of individual morphotypes.

The holotype of *T. verneuilanum* (EM 15159) was collected by Verneuil at Buttonmold Knob, 7 mi south of Louisville, Bullitt County, Kentucky and is housed in the Institut de Paléontologie, Paris, France. No other primary type material is known to exist.

The following topotype collections studied, all from Buttonmold Knob, are housed in the US National Museum of Natural History, Washington, D. C., USA:

USNM 88112—5 sectioned and 16 unsectioned specimens collected by A. F. Foerste.
USNM 140348—2 sectioned specimens and one unsectioned specimen studied by E. C. Stumm (1948).

USNM 415745—4 unsectioned specimens collected by R. S. Bassler.

USNM 415746—17 sectioned and 17 unsectioned specimens.

Additional topotypes include 13 unsectioned specimens collected by L. R. Laudon and housed at the University of Wisconsin Geology Museum (UW 4006). These specimens were not studied in detail.

Specimens from the New Providence Shale Member at nearby localities, all housed at the US National Museum of Natural History, Washington, D. C. are:

USNM 88138—3 sectioned and 8 unsectioned specimens collected by A. F. Foerste 0.5 mi south of Acton, Taylor County, Kentucky.

USNM 37459—4 sectioned and 12 unsectioned specimens collected by C. L. Rominger south of Danville, Boyle County, Kentucky.

USNM 415747—one sectioned and 10 unsectioned specimens from a knob just south of Louisville, Bullitt County, Kentucky (possible topotypes).

SYSTEMATIC DESCRIPTIONS

Suborder *Metriophyllina* Spassky, 1965

Family ?*Petraiidae* de Koninck, 1872

Discussion.—The systematics of small, aulate solitary corals remain open for discussion in spite of several progressive studies by Weyer (1971, 1977, 1978a, b, 1984) and the recent general revision by Hill (1981). Weyer (1978a, b) discussed the

relationship to *Metriophyllidae* Hill, 1939 of *Neaxon* Kullmann, 1965, *Neaxonella* Weyer, 1978, and other genera having no contratingent septa, and Hill (1981) distinguished these corals as a separate subfamily Neaxoninae.

Restudy of the type material of *Lindstroemia* Nicholson and Thomson, 1876 by Scrutton and Weyer (in press) and study of the type material of *Petraia decussata* Münster, 1839 by Weyer (in preparation) throws new light on the systematics within aulate solitary corals. Both the family concepts and the generic content of individual families and subfamilies have to be reconstructed to a large degree. Knowing that the present taxonomic status is unacceptable, but having no published data, we decided to use the family name *Petraiidae* de Koninck, 1872, in a broad sense, to place the genus *Trochophyllum* Milne-Edwards and Haime, 1850, revised herein. Weyer (letter to J. F., July 2, 1987) has suggested: "It seems the best to put *Petraia* just with its closest generic neighbours into the subfamily *Petraiinae*, which included further: *Neaxonella*, *Paliaxon*, *Czarnockia* (with synonyms *Friedbergia*+*Famenelasma*), *?Hillaxon*." This generic relationship is very close to the content of subfamily Neaxoninae Hill, 1981, but the priority of *Petraiinae*, which will be most probably validated in a year or two, makes the use of *Neaxoninae* ambiguous. We thus decided not to use a subfamily name, but to point out the relationships of *Trochophyllum* to the genera listed by Weyer in his letter and to most of the genera included by Hill (1981) in her subfamily Neaxoninae.

Genus *Trochophyllum* Milne-Edwards and Haime, 1850

Synonymy:

1850. *Trochophyllum* Milne-Edwards and Haime: 1 xvii.
 1851. *Trochophyllum* Milne-Edwards et J. Haime: 166, 356.
 non 1856. *Trochophyllum* Milne-Edwards et Haime; Eichwald: 102—103.
 1860. *Trochophyllum* Milne-Edwards et J. Haime; Milne-Edwards: 359.
 non 1859, 1860. *Trochophyllum* M. Edw. Haime; Eichwald: 528—529.
 1861. *Trochophyllum* Edwards and Haime; Fromental: 291.
 part. 1891. *Zaphrentis*; Miller: 10—12.
 part. 1892. *Zaphrentis*; Miller: 620—622.
 1898. *Trochophyllum* Milne-Edwards and Haime; Weller: 636.
 1935. *Crassiphyllum* Grove: 368.
 1940. *Trochophyllum* Edwards et Haime; Lang, Smith, and Thomas: 135.
 1944. *Crassiphyllum* Grove; Hudson: 359, 360.
 non 1944. *Permia* Stuckenberg; Hudson: 359.
 1948. *Trochophyllum* Edwards and Haime; Stumm: 71.
 1948. *Crassiphyllum* Grove; Stumm: 71.
 1950. *Trochophyllum* Edwards and Haime; Wang: 204.
 part. 1956. *Trochophyllum* M. Edw.-H.; Hill: F258.
 1956. *Crassiphyllum* Grove; Hill: F258.
 non 1956. *Permia* Stuckenberg; Hill: F258.
 part. 1958. *Trochophyllum* Milne-Edwards and Haime; Easton: 15—20.
 1958. *Crassiphyllum* Grove; Easton: 15.
 non 1958. *Permia* Hudson; Easton: 15.
 1962. *Trochophyllum* Edwards et Haime; Soshkina, Dobrolyubova, and Kabakovich: 322.
 1962. *Crassiphyllum* Grove; Soshkina, Dobrolyubova, and Kabakovich: 322.
 1967. *Trochophyllum* Edwards and Haime; Pickett: 7.
 1967. *Crassiphyllum* Grove; Pickett: 7.

- part. 1967. *Trochophyllum* M. Edwards et Haime; Ivanovskiy: 44—46.
 1970. *Trochophyllum* Edwards and Haime; Flügel: 290—291.
 1970. *Trochophyllum* Edwards and Haime; Hill and Jell: 17, 21.
 1970. *Crassiphyllum* Grove; Hill and Jell: 17, 21.
 1973. *Trochophyllum* Edw.-H.; Cotton: 213.
 1973. *Crassiphyllum* Grove; Cotton: 55.
 1976. *Trochophyllum* M.-Edwards et Haime; Ivanovskiy: 178.
 1976. *Crassiphyllum* Grove; Ivanovskiy: 48.
 1981. *Trochophyllum* Milne-Edwards and Haime; Hill: F198.
 1981. *Crassiphyllum* Grove; Hill: F198.
 1982. *Trochophyllum* Edwards and Haime; Wu and Zeng: 144.
 part. 1982. *Crassiphyllum* Grove; Wu and Zeng: 143—144.
 part. 1983. *Trochophyllum* Edw.-H.; Cotton: 167.
 part. 1983. *Crassiphyllum* Grove; Cotton: 47.
 1984. *Trochophyllum* Edw.-H.; Cotton: 176.
 1984. *Crassiphyllum* Grove; Cotton: 46.
 non 1985. *Trochophyllum*; Guo: 69.

Type species.—*Trochophyllum verneuilanum* Milne-Edwards and Haime, 1851: 357, pl. 5: 6, 6a. The earlier name *T. verneuli* Milne Edwards and Haime (1850: 1 xvii and 1850: 166) is a *nomen nudum* and cannot be considered the valid name for the species.

Diagnosis.—Small, nondissepimentate horn corals having the cardinal septum on convex side of corallite; septa of two cycles, but minor septa developed at most as foundations only; cardinal septum in calice thinner and lower (shorter in cross section) than other major septa, reaching stereoplasmic wall of aulos both in calice and beneath it; counter septum commonly equal to counter lateral septa, sometimes slightly longer; alar septa indistinguishable by length and thickness; aulos originated from termination of growth of axial ends of 6—8 major septa early in ontogeny; aulos of stereotheca-type at maturity, commonly filled in with stereoplasm; tabularium normal; axial parts of tabulae almost horizontal, not seen in areas of complete stereoplasmic infilling, their peripheral parts inclined highly upward toward aulos and major septa; microstructure of foundations of septa lamellar, of septal blades fine trabecular.

Previous opinions on systematic relationships.—Stumm (1948: 71), the first author to comment on the systematic relationships of *Trochophyllum*, concluded from a study of topotypes that *Trochophyllum* was a senior synonym of *Crassiphyllum* Grove. Grove (1935: 368) based *Crassiphyllum* on *Zaphrentis declinis* Miller, which is from the same stratigraphic unit as *T. verneuilanum*, only a short distance north of the type locality of the latter. Examination by the junior author of the illustrations and descriptions of *Z. declinis* by both Miller (1891, 1892) and Grove (1935) reveals that the two species are identical. Hudson (1944: 359, 360), although he did not mention *Trochophyllum*, concluded that *Crassiphyllum* Grove, 1935 is a junior synonym of *Permia* Stuckenberg, 1895. Hill (1956: F258) regarded *Permia* and *Crassiphyllum* as junior synonyms of *Trochophyllum*.

Easton (1958: 15—20), in an attempt to consolidate existing laccophyllid coral genera, regarded *Trochophyllum* as a genus that included the subgenera *Trochophyllum*, *Barrandephyllum* Počta, *Permia* Stuckenberg, and unnamed subgenus based on *Laccophyllum turbinatum* Gorskiy. Easton distinguished these subgenera on variations in the number of orders of septa and tabulation vs. non-tabulation of the aulos. Te regarded *Crassiphyllum* as a junior synonym of *Trochophyllum*.

Soshkina, Dobrolyubova, and Kabakovich (1962: 328), based on a study of Stuckenberg's types, concluded that *Permia* is merely an early stage of *Aulophyllum*

Milne-Edwards and Haime, thus nullifying previous attempts to use the name *Permia* for small aulate solitary corals in the Carboniferous. Although Pickett (1967: 7) does not seem to have been aware of the work of Soshkina, Dobrolyubova, and Kabakovich, he concluded that *Trochophyllum* and *Permia* are not congeneric, based on a study of topotypes of *Trochophyllum*. Pickett pointed out that Grove's illustrations of *Crassiphyllum* were similar to topotypes of *Trochophyllum*, but he did not have topotypes of *Crassiphyllum* for comparison and did not make a final judgment on this question.

Ivanovskiy (1967: 44—45), also seemingly unaware of the work of Soshkina, Dobrolyubova, and Kabakovich, regarded *Permia* Stuckenberg as a junior synonym of *Trochophyllum*. He also included in *Trochophyllum* corals assigned to *Laccophyllum* Simpson and *Barrandeophyllum* Pořta by Gorskiy (1932), Voynovskiy-Kruger (1934), and Volkova (1941).

Hill and Jull (1970: 17, 21) placed *Trochophyllum*, *Permia*, and *Crassiphyllum* questionably in the synonymy of *Syringaxon* Lindstrom, but reserved final judgment until the types of these genera are redescribed. Hill's final judgment was expressed in 1981 (p. F198), when she returned to Stumm's (1948) conclusion that *Trochophyllum* is a discrete genus that includes *Crassiphyllum* Grove as a junior synonym.

Fedorowski's (1971: 24) careful restudy of Stuckenberg's type material of *Permia invanowi* unequivocally confirmed the previous opinion of Soshkina, Dobrolyubova, and Kabakovich (1962: 328) that the type species of *Permia* is a young stage of *Aulophyllum* and that *Permia* is a junior synonym of *Aulophyllum*.

More recently, Wu and Zeng (1982: 143—144) attempted to revive *Crassiphyllum* as a discrete genus, based on the interpretation that *Crassiphyllum* has an aulos and *Trochophyllum* does not. This may have influenced Guo (1985) in his attempt to use *Trochophyllum* to describe some corals from the Carboniferous of Inner Mongolia (see remarks below).

Disposition of species assigned previously to Trochophyllum.—Eichwald (1856: 102—103; 1859: 4, fig. 10; 1860: 528—529) described a coral from the Visean? at Kaluga City, Russia, under the name of *Trochophyllum radiatum*. Fedorowski and Gorianov (1973: 50—52) redescribed Eichwald's type specimen and assigned it to *Bothrophyllum inostranzewi* (Stuckenberg).

As mentioned above, *Zaphrentis declinis* Miller, 1891, type species of *Crassiphyllum* Grove, is regarded by us a junior synonym of *Trochophyllum verneuilianum* on examination of Miller's (1891, 1892) and Grove's (1935) descriptions and illustrations.

Easton (1958: 16—18) placed the following species in *Trochophyllum*:

- Trochophyllum (Trochophyllum)* sp.—Lower Carboniferous (Mississippian), Sonora, Mexico
- Trochophyllum (Barrandeophyllum)* sp.—Lower Carboniferous (Mississippian), Sonora, Mexico
- Barrandeophyllum choniukouense* Grabau—Lower Carboniferous (Visean), Kansu, China
- Barrandeophyllum compressum* Grabau—Lower Carboniferous (Visean), Kansu, China
- Barrandeophyllum disjunctum* Grabau—Lower Carboniferous (Visean), Kansu, China
- Barrandeophyllum perplexum* Pořta—Middle Devonian, Bohemia
- Laccophyllum turbinatum* Gorskiy—Lower Carboniferous, Kirghiz Steppe, USSR
- Permia iwanowi* Stuckenberg—Lower Carboniferous, Ural Mountains, USSR

Permia caverna Hudson—Lower Carboniferous (Visean), Yorkshire, England
Permia carbonaria Hudson—Lower Carboniferous (Visean), Yorkshire, England.

The junior author examined Easton's specimens from Sonora (USNM 127949 and 127952) and found that neither of these has the true characters of *Trochophyllum*. Easton's *Trochophyllum* (*Barrandeophyllum*) sp. is an undescribed species of *Amplexocartnia* Soshkina. Easton's *Trochophyllum* (*Trochophyllum*) sp. is a peculiar coral unlike any known from North America. It has a prominent, sinuous, atabulate, axial tube that is not constructed from the axial ends of the major septa. This tube originates about 5 mm below the calice and extends upward about 3 mm above the calice floor. The junior author interprets this structure as the tube of a symbiotic worm inserted in a specimen of *Amplexizaphrentis* Vaughan.

The three Chinese Visean species described by Grabau (1928) and placed by Easton (1958: 16–18) in *Trochophyllum* are somewhat similar to each other in the mature growth stages but must be discussed separately because of some important differences and/or incomplete descriptions. *Barrandeophyllum choniukouense* (Grabau 1928: immature stage illustrated on pl. 2: 19b, c) may be compared to *Trochophyllum* sp. 1 of this report, but not in its calice and the subcalicular part of the corallite (Grabau 1928: pl. 2: 19d, upper). The aulos, possibly tabular and incomplete in the mature corallite, disappears in the calice, where the counter septum is clearly elongated. This character is absent from the ontogenetically younger part of the corallite. Illustrations of the ontogenetically earliest stages are probably oriented with the cardinal septum toward the left (Grabau 1928: pl. 2: 19a, b). The early ontogeny and microstructure of the septa are unknown. These characters, as well as the differences and uncertainties mentioned above, seem adequate for excluding Grabau's specimen from *Trochophyllum*, at least for the present. The inadequacy of the description of the paratype of this species and the lack of illustrations make any comments on it baseless.

Barrandeophyllum compressum is certainly an aulose coral in its early growth stage, and the earliest illustrated section (Grabau 1928: pl. 3: 8b) resembles some early stages of *Trochophyllum*. However, no information concerning the earliest growth stage of that species and the microstructure of its septa has been presented. Also, a true aulos may not be present in the early mature part of the corallite (Grabau 1928: pl. 3: 8c), where the major septa seem to only surround the free axial area. The arrangement of major septa is radial, without a false counter fossula, and the cardinal septum in the calice (Grabau 1928: pl. 3: 8d) does not differ from the adjacent major septa by length and/or thickness. Although affinity of *B. compressum* to *Trochophyllum* on the family level seems probable, we do not consider it congeneric with the latter genus.

Grabau (1928: 95) distinguished his new *Barrandeophyllum disjunctum* by "the inner tabulae ... which in the later stages become more or less independent", but "since the calyx is however unknown it cannot be determined to what extent this tube may project into it". Although we cannot be certain, the arrangement of the cross sections of tabulae, especially those seen in Grabau (1928: pl. 3: 1d) indicate that there is no true aulos, at least in the upper part of the corallite, where the tabulae are incomplete and dome-like. Similarly, as in the two other Grabau species included by Easton in *Trochophyllum*, the arrangement of major septa is radial or semi-radial, and the microstructure of the septa and early ontogeny are unknown. Therefore, we cannot find a basis for placing these Grabau species in *Trochophyllum*.

We come to a similar conclusion for *Laccophyllum turbinatum* Gorsky 1932, which shows disintegration of the aulos in the mature corallite and the cardinal

septum almost indistinguishable, features that exclude this species from *Trochophyllum*.

Permia carbonaria Hudson, 1944 has contratingent minor septa, which excludes it from further consideration as a species of *Trochophyllum*, although Hudson placed that species intermediate between two of his other species, *P. cavernula* Hudson, 1943 and *P. caverna* Hudson, 1944 because of the slight underdevelopment of that character. We can offer no final opinion concerning that phylogenetic line because the microstructure of the septa of those species, as well as their calices and early ontogenies, are unknown. If Hudson's (1943) reconstruction is correct, we have a strong argument against considering *Permia caverna* Hudson, 1944 a species of *Trochophyllum*, or even a species related to it within the same family. There are examples in the coeval European coral fauna (e.g., *Claviphyllum* Hudson, 1942) in which the presence of minor septa is variable and consequently is rejected from consideration as a generic character.

Three species described by Iwanowski (1967) under *Trochophyllum* are difficult to identify because of inadequate description and illustration. Ivanovskiy's *Trochophyllum spinosum* (Voynovskiy-Krieger, 1934) seems to belong to *Amplexocarinia* Soshkina. The longitudinal section of the first of two specimens illustrated by Ivanovskiy (1967: pl. 3; 1b) is probably oriented upside-down. The transverse section of the second specimen (pl. 3: 2a) shows similarity to *Nicholsonia* (?) of Voynovskiy-Krieger (1934) (seen by J. F.) and to *Trochophyllum* in the arrangement of major septa, which are inclined slightly toward the cardinal septum. However, the longitudinal section of Ivanovskiy's specimen shows no aulos, which excludes it from *Trochophyllum*. In contrast, Voynovskiy-Krieger's *Nicholsonia* (?) sp. has not only a slightly shortened cardinal septum but also a true aulos that is almost completely filled in with stereoplasm. This Lower Tournaisian specimen from the Ural Mountains is morphologically very close to *Trochophyllum*; we exclude it from the synonymy of that genus mainly because of the lack of data concerning its ontogeny and microstructure. Specimens described by Voynovskiy-Krieger (1934) as *Meniscophyllum uralicum* and *M. uralicum aperta* (seen by J. F.) show some similarities to *Trochophyllum* but must also be carefully redescribed before any final decision on their taxonomy can be made. The junior author believes that the widely open cardinal side of the axial zone and lack of stereoplasmic filling in the axial region of the mature corallite exclude these corals from *Trochophyllum*. *Trochophyllum annae* Ivanovskiy, 1967 and *T. sp.* Ivanovskiy, 1967 show no characters of *Trochophyllum*. Their true affinities cannot be deduced from their original descriptions and illustrations.

Laccophyllum fossulatum Volkova, 1941 was included in synonymy with *Trochophyllum* by Ivanovskiy (1967). This ambiguous, poorly illustrated species, described by Volkova (1941) on a single, incomplete corallite from the Lower Tournaisian of Kazakhstan, cannot be discussed seriously with the information available. We were not even able to orient its two sections with full confidence.

Crassiphyllum irregulare Wu and Zeng (1982: 144, pl. 1: 1—3) from the Lower Carboniferous of Xinjiang, China, is similar to *Trochophyllum* in having an open axial zone at some stage of its growth and in its wedge-shaped peripheral ends of major septa, but important details of this coral are not determinable from Wu and Zeng's descriptions. No longitudinal sections of this coral were illustrated.

Guo (1985) distinguished two new species of *Trochophyllum*, *T. grossum* and *T. irregulare*, and left one species in open nomenclature (*T. sp.*), all from the Xieertala Formation of Inner Mongolia. The age of the formation, originally determined as Late Carboniferous on the basis of brachiopods, was regarded by Guo to be Early Carboniferous by comparing the coral assemblage to that of Zone Z2 of

Britain and to that of the Keokuk Limestone or New Providence Shale Member of the Midcontinent region in the United States. The corals described and illustrated by Guo appear to us to have a Middle or Upper Carboniferous character comparable to the fauna of that age from the Donetz basin (Fomichev 1953), Spain (de Groot 1963; Rodriguez 1984) and the Carnic Alps and Yugoslavia (noted by Fedorowski 1981).

We cannot determine the identity of Guo's *Trochophyllum* sp. because his illustration and description are inadequate for detailed analysis of its affinities. We can conclude only that the specimen does not show any characters of *Trochophyllum*. *T. grossum* and *T. irregulare* probably represent a single species that we would place within *Bradyphyllum* Grabau, 1928 close to *B. oppositum* Fomichev, 1953, or even closer, to "*Rotiphyllum*" *exile* de Groot, 1963.

In summary, we have not been able to find in the literature any species, other than the type species and its synonym, *Zaphrentis declinis* Miller, that we can conclusively assign to *Trochophyllum*. However, corals described by Voynovskiy-Krieger (1934) from the Tournaisian of the Ural Mountains under the names *Nicholsonia* (?) sp., *Meniscophyllum uralicum*, and *M. uralicum apertum* cannot be ruled out without further study of their type material. Similarly, *Crassiphyllum irregulare* Wu and Zeng, 1982 needs further investigation before its generic identity can be determined.

Relationships to other genera.—Only a few described genera, namely *Neaxon* Kullmann, 1965, *Neaxonella* Weyer, 1978, *Nicholsoniella* Soshkina, 1952, and to a lesser degree also *Amplexocarinia* Soshkina, 1928, *Nalivkinella* Soshkina, 1939, and *Parallelyntia* Soshkina, 1936, can be considered as similar and/or related to *Trochophyllum* Milne-Edwards and Haime, 1850. The similarity of *Neaxon* to *Trochophyllum* sp. 1 is especially striking because in this species, the major septa are almost equal in length and the aulos has no stereoplasmic infilling. Some of the specimens assigned to this species (e.g. USNM 37459) seem to lack the characteristic foundations of septa with distinct growth lines, although the absence of this character may be the result of recrystallization. The main features that distinguish *Neaxon* from *Trochophyllum* are: (1) lack of shortening of the cardinal septum even in sections of the uppermost parts of calices (cardinal septum equal in height to other major septa), (2) the development of true minor septa having a median dark line, (3) the monacanthine microstructure of the septa, reflected in the comb-like morphology of the inner ridges of septa in calices (e.g., Weyer 1971: pl. 6: 1), (4) lack of a clear distinction between the initial (foundations) and mature stages of major septa, and (5) origin of the aulos.

Neaxonella differs from *Neaxon* primarily in having the cardinal septum shortened in cross section in the upper part of the calice, i.e., lower than other major septa (Weyer 1978: 293), which causes it to resemble *Trochophyllum* even more than *Neaxon* does. The main characters distinguishing *Neaxonella* from *Trochophyllum* are the same as points 1–4 listed above for *Neaxon*, and the bifurcated tabularium. Contrary to Weyer's (1978) opinion, this may be the main difference of this genus from *Neaxon*, because the length (= height) of the cardinal septum may vary in the Neaxoninae (= probably Petraininae de Koninck). An additional distinguishing character is the zaphrentoid or similar arrangement of major septa that occurs in many, if not all, corallites, even when the aulos has a contemporary or earlier origin (e.g., Weyer 1978: pl. 1: 4; pl. 3: 2, 3; pl. 4: 1, 2; pl. 5: 5; pl. 6: 2, 4, 5, 6; pl. 7: 1, 2). The arrangement of septa occurring in the late neanic stage of many corallites of *Trochophyllum* could be called anti-zaphrentoid because of the opening of the half-aulos toward the separated counter septum (pl. 8: 3a). Another important difference

is the slightly different origin of the aulos, if Weyer's (1978a: pl. 6: 1—3) illustrations can be considered typical of *Neaxonella*.

We generally agree with the comprehensive discussion by Weyer (1978b) on the relationship of *Nicholsoniella bashkirica* Soshkina, 1952 to *Neaxon* and *Neaxonella*. The well developed minor septa and the appearance of an incomplete row of dissepiments in the latest growth stage of *Nicholsoniella* are distinguishing features of this genus, although its morphology in the subcalicular region is very similar to that of *Trochophyllum*. However, the development of dissepiments in *Nicholsoniella*, an advanced phylogenetic character, prohibits considering *Trochophyllum* (Early Carboniferous) as descendant of *Nicholsoniella* (Late Devonian).

Paralleynia Soshkina, 1936 and *Amplexocarinia* Soshkina, 1928 were recently discussed in detail by Fedorowski (1986). The earliest ontogeny, microstructure, and calice morphology of *Amplexocarinia* are unknown, but its subcalicular morphology, in which the cardinal septum is permanently equal to other major septa and a complete aulos is not present, differs distinctly from the mature corallite of *Trochophyllum*.

The aulos in *Paralleynia* appears comparatively late in its ontogeny, but its origin has not been studied in detail. The zaphrentoid arrangement of septa in the early ontogeny suggests that the aulos originated by withdrawal of the inner ends of the septa from the corallite axis without breaking direct contact of their middle lines. This can be confirmed, to some extent, by the morphology of the mature growth stage. The morphology of the aulos in *Paralleynia* can thus be compared to the late neanic stage of *Trochophyllum*, except that the aulos is never opened toward the counter septum in *Paralleynia*, but is either closed or open toward a shortened cardinal septum. As in *Trochophyllum*, however, the aulos extends high in the calice (cf. Soshkina 1936: fig. 7). The most important distinguishing characters of *Paralleynia* are: (1) the long-lasting zaphrentoid stage in ontogeny, (2) the minor septa well developed at least near the counter septum, (3) the aulos at least temporarily open toward the cardinal septum and never toward the counter septum, and (4) the absence of two cycles of growth of the major septa. The microstructure of the septa in *Paralleynia* is unknown. Despite these differences, *Paralleynia* seems morphologically close to *Trochophyllum*. We are unable to determine on present evidence whether these two corals are close relatives or only morphological analogs.

The genus *Nalivkinella* Soshkina, 1939 is mentioned herein mainly because of its similarity to *Amplexocarinia* Soshkina, 1928, especially during early ontogeny. Lack of an aulos in the mature part of its growth and a completely different arrangement of peripheral tabulae in longitudinal section make it readily distinguishable from *Trochophyllum* sp. 1.

Trochophyllum verneuilanum Milne-Edward and Haime, 1851
(pls. 1—9, 11—12; figs. 1—5, 8—11)

Synonymy:

1850. *Trochophyllum Verneuili* Milne-Edwards and Haime: lxvii [*nomen nudum*].
 1851. *T. verneuili* Milne-Edwards and Haime: 166 [*nomen nudum*].
 1851. *Trochophyllum verneuilanum* Milne-Edwards and Haime: 357, pl. 5: 6, 6a.
 1860. *Trochophyllum Verneuilanum* Milne-Edwards et J. Haime; Milne-Edwards: 359.
 1861. *T. verneuili-T. Verneuilanum* Edwards et Haime; Fromentel: 291—292.
 1891. *Zaphrentis declinis* Miller: 12, pl. 1: 25, 26.
 1892. *Zaphrentis declinis* Miller: 622, pl. 1: 25—26.
 1898. *Trochophyllum verneuilanum* Milne-Edwards and Haime; Weller: 636.

1935. *Crassiphyllum declinis* (Miller); Grove: 369—370, pl. 9: 9—11; pl. 12: 12—16.
1940. *T. verneuili* Edwards and Haime; Lang, Smith, and Thomas: 135.
1940. *Zaphrentis declinis* Miller; Hudson: 360.
1948. *Trochophyllum verneuili* Edwards and Haime; Stumm: 71, pl. 17: 25—29.
1950. *Trochophyllum verneuili* Edwards and Haime; Bassler: 214.
1956. *T. verneuili*; Hill: 258.
1958. *Trochophyllum verneuili* Milne-Edwards and Haime; Easton: 15.
1958. *Trochophyllum (Trochophyllum) declinis* (Miller); Easton: 16.
1967. *Trochophyllum verneuili* Edwards and Haime; Pickett: 7, pl. 1: 12.
1967. *Trochophyllum verneuilanum* Milne-Edwards et Haime; Ivanovskiy: 44.
1970. *T. verneuili* Edwards and Haime; Hill and Jell: 21.
1970. *Zaphrentis declinis* Miller; Hill and Jell: 21.
1970. *T. verneuili* Edwards and Haime; Flügel: 290.
1970. *Zaphrentis declinis* Miller; Flügel: 67.
1970. [*T.*] *verneuili*; Cotton: 213.
1973. *Zaphrentis declinis* Miller; Cotton: 55.
1974. *Trochophyllum verneuilanum* Milne-Edwards and Haime; Sando: 25.
1974. *Zaphrentis declinis* Miller; Sando: 8.
1976. *T. verneuili*; Ivanovskiy: 178.
1976. *Zaphrentis declinis* Miller; Ivanovskiy: 48.
1981. *T. verneuili*; Hill: F198.
1981. *Zaphrentis declinis* Miller; Hill: F198.
1982. *Zaphrentis declinis* Miller; Wu and Zeng: 144.
1983. *T. verneuili* E. and H.; Cotton: 167.
1983. *Zaphrentis decline* Mil.; Cotton: 47.
1984. [*T.*] *verneuili*; Cotton: 176.
1984. *Zaphrentis declinis* Miller = *Crassiphyllum decline* (Miller); Cotton: 46.
1985. *Trochophyllum verneuilanum* Milne-Edwards and Haime; Kammer: Tables II and VI.

Material studied.—EM 15159; USNM 88112, 88138, 37459, 140348, 415745, 415746, 415747: 111 specimens (33 sectioned), see earlier section on material studied and occurrence.

External characters.—All corallites are narrowly horn-shaped, having the cardinal septum located on the convex side of the corallite. The external wall is thin, sometimes slightly, between major septa; it bears both growth striae and septal furrows of the major and minor septa (pl. 4: 2b; pl. 1b, 3). In most specimens, the corallite is free of matrix, and only thick, peripheral portions of septa are seen on the corallite surface (pl. 4: 1b; pl. 5: 6; pl. 6: 2b). The external wall may be so thin that septal furrows are very weakly marked, but septa themselves are visible through it (pl. 4: 1b; pl. 6: 1b). The stronger growth striae may be imprinted on the peripheral parts of septa, being visible there after dissolution of the epitheca (pl. 5: 6; pl. 6: 2b). None of the specimens has a talon, attachment processes, or attachment surfaces; this is true not only for weathered corallites, but also for those that have the external surface fairly well preserved. Many specimens have deep constrictions. Some show more or less deep rejuvenations (pl. 4: 2b; pl. 6: 1b, 3).

Diagnosis.—*Trochophyllum* having n:d ratio as much as 23:9.8 in calice; aulos filled in with stereoplasm, rarely open in neanic stage only; major septa inclined slightly toward cardinal septum.

Description of holotype.—The outer part of the corallite is composed mainly of light brown microcrystalline silica; only the axial part of the interior is unsilicified calcite. The specimen is nearly free of matrix, except for small amounts of shale that were removed mechanically from between septa in the calice.

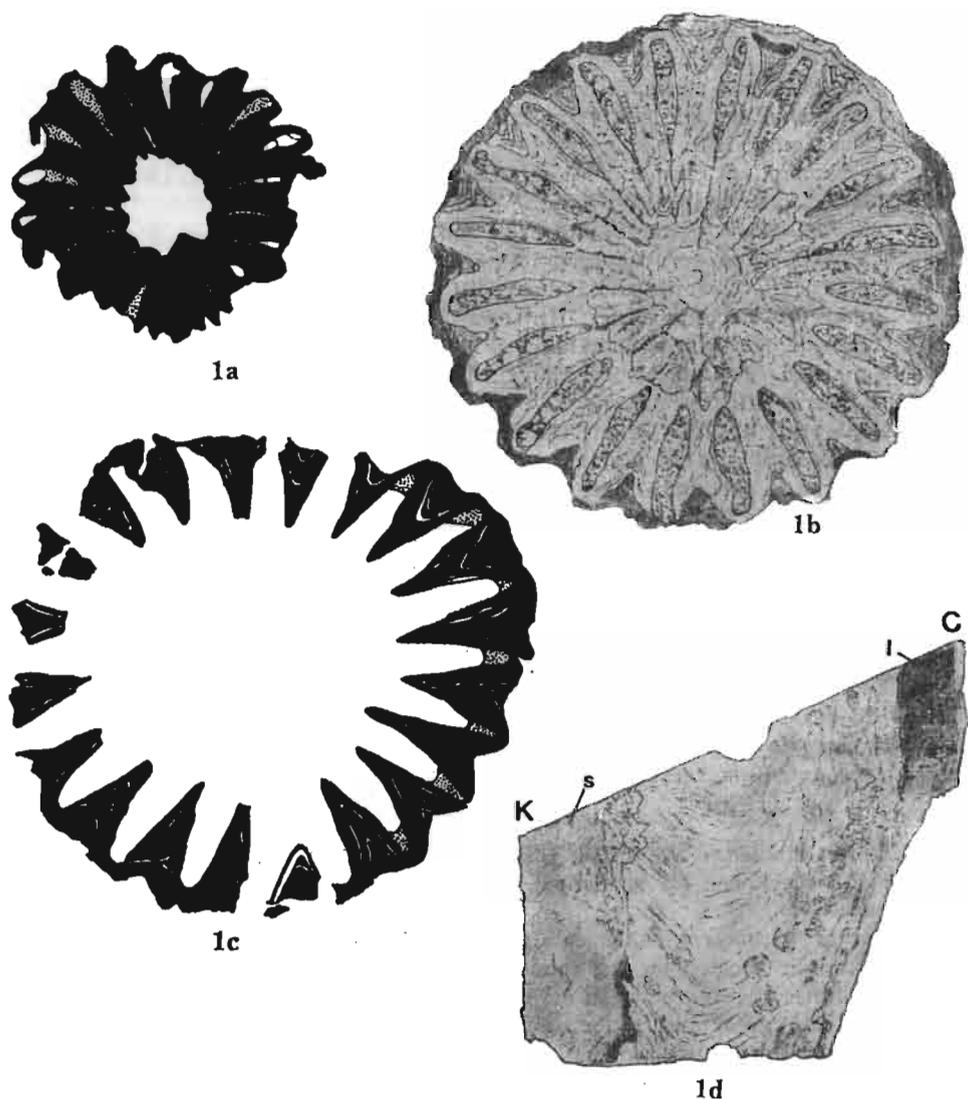


Fig. 1. *Trochophyllum verenuilanum* Milne-Edwards and Haime, 1850. EM 15159, holotype: a transverse thin section, late neanic/early ephebic stage (slightly schematized), b transverse thin section, lower part of calice, c transverse thin section, lower part of calice, d longitudinal thin section in cardinal-counter plane; all $\times 9$ (b, d by W. J. Sando)

The corallite is curved-ceratoid in form and lacks epitheca, which was probably thin and removed by abrasion (pl. 1: 1a—d). The exterior is marked by pronounced interseptal ridges as much as 0.5 mm wide and 0.8 mm high, probably exaggerated by abrasion. The tip is broken off; the diameter of the broken apex is 5.6 mm, where 18 major septa are preserved. Dimensions of the corallite are given in terms described by Sando (1961):

Alar diameter (d_1) = 10.2 mm

Cardinal-counter diameter (d_2) = 9.1 mm

Length (L) = 18.3 mm

Cardinal length (1) = 23.0 mm

Calicular angle (α) = 20 degrees

The calice (pl. 1: 1a) is 4 mm in maximum depth, measured at the axis of the corallite. The cardinal septum is short and located on the convex side of the corallite. The counter septum is slightly longer than other major septa. Alar septa are not distinguishable on length. The other major septa are 3–3.5 mm long and extend to an axial depression 2.5 mm in diameter and 0.5 mm deep. Twenty major septa are distinguishable in the calice; minor septa are not distinguishable. The septa are wedge-shaped, tapering toward the axis of the corallite.

A transverse thin section (EM 15159c, fig. 1a), cut at the strongly corroded, broken tip of the corallite, shows 18 major septa that fall short of the axis, leaving an open axial zone about 2 mm in diameter consisting of cryptocrystalline silica and open space where the coral structure has been leached out. No minor septa are visible. The exterior of the corallite has been deeply corroded, and most of the peripheral parts of the septa have been removed. These open spaces are filled with caliche, and the septa are replaced by cryptocrystalline silica. The section is about 6 mm in diameter.

A transverse thin section (EM 15159b; fig. 1b; pl. 3: 3) shows the epehebic internal structure just below the floor of the calice at an alar diameter of 9.5 mm. The septal complement at this stage is 20, including a slightly shorter and thinner

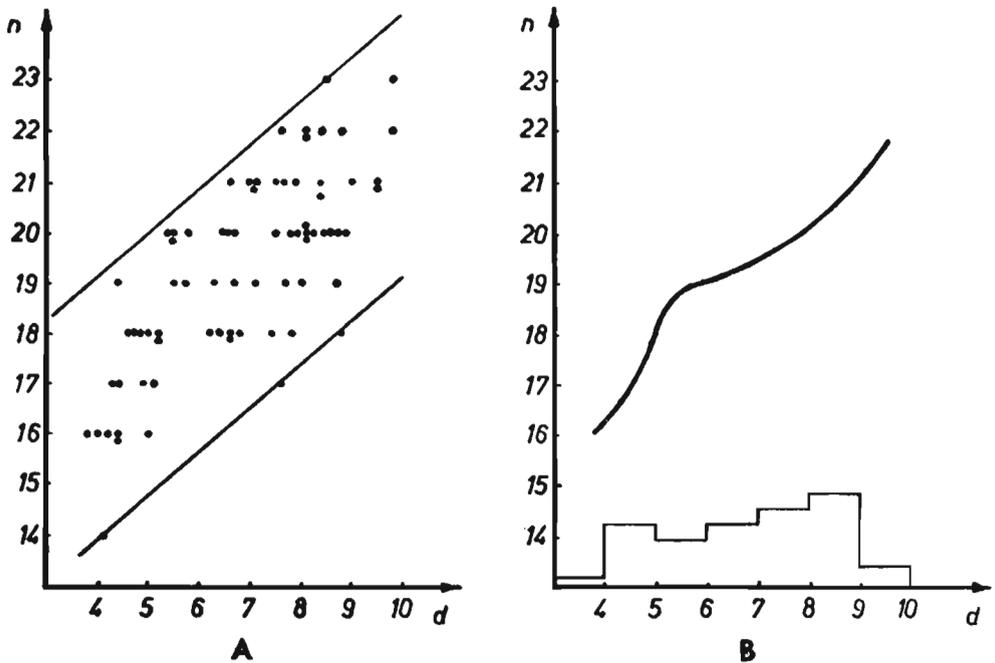


Fig. 2. Plots of ratio of number of major septa to corallite diameter (n:d) in *T. verneuillanum* Milne-Edwards and Haime, 1850. A field of individual measurements of number of major septa (n, on vertical axis) and corallite diameter (d, on horizontal axis); B plot of mean n:d ratio and histogram (bottom) showing numbers of corallites in diameter classes; change in slope of median line corresponding to minimum in number of corallites in histogram indicates possible existence of two species or subspecies in the material here included in *T. verneuillanum*.

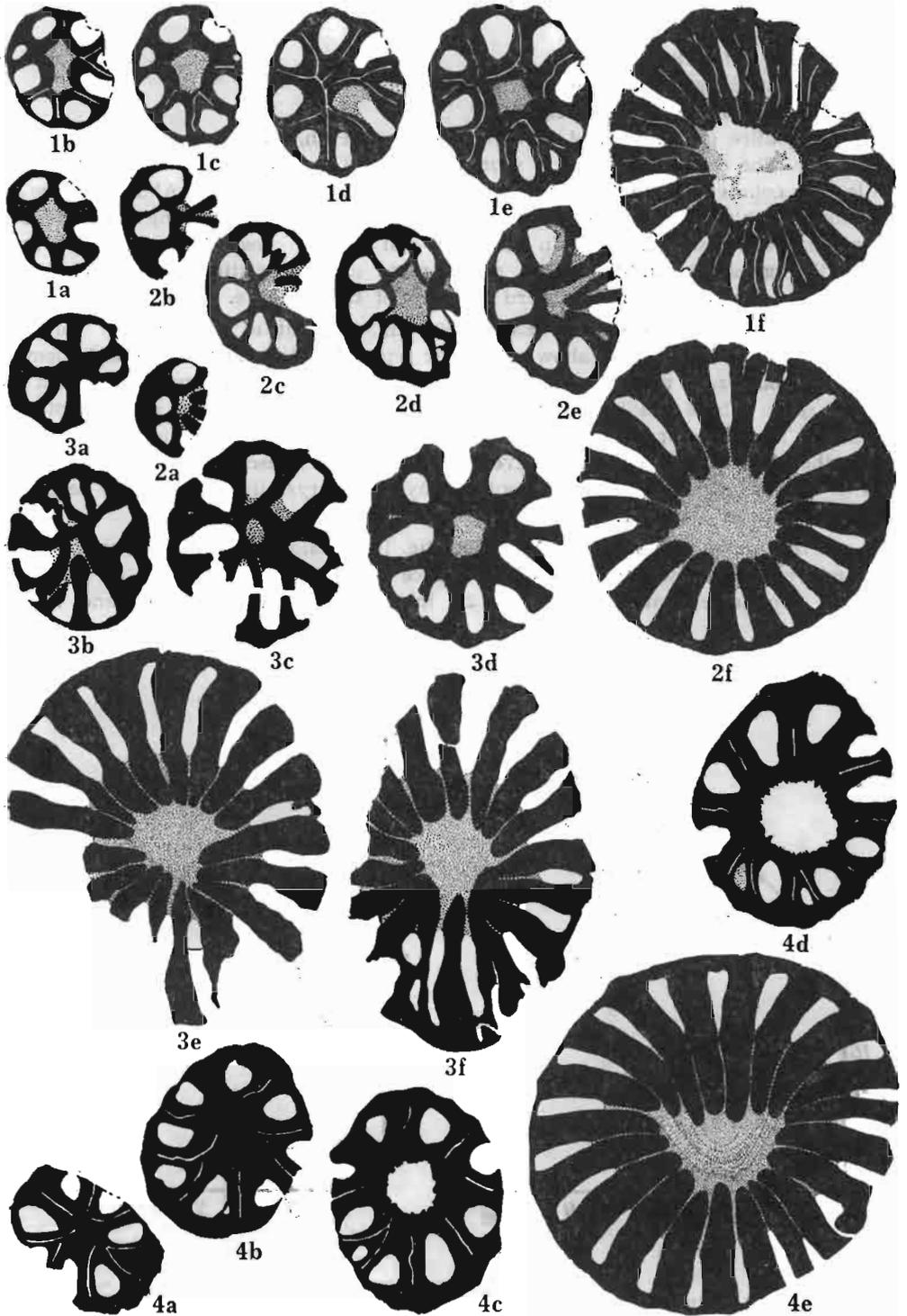


Fig. 3. *Trochophyllum verneuillanum* Milne-Edwards and Haime, 1850. Transverse thin sections. 1. USNM 415746C, topotype: a—c early neanic stage, showing aulos filled in with stereoplasm and bordered by primary parts of major septa, $\times 15$; d early neanic stage, showing disappearance of aulos, $\times 15$; e neanic stage, showing

cardinal septum and a slightly longer and thicker counter septum. Alar positions are almost indistinguishable, and no minor septa are present in the lumen. The lumen can be divided into two zones of different mineral composition, an axial zone in which original microstructure of the septa and stereoplasm is preserved as microcrystalline calcite, and an outer zone in which the septa have been replaced by spherulitic cryptocrystalline silica in which only vestiges of the original microstructure remain preserved.

The septa do not reach the axis of the corallite, leaving an open area about 2 mm in diameter filled by stereoplasm (pl. 2: 1b). The stereoplasm was deposited in concentric layers composed of fibers that are perpendicular to the layering. No tabulae are visible. The axial ends of the septa are poorly defined and slightly swollen. Septal microstructure of secondary sheets of septa and their foundations is of the lamellar type of Kato (1963). Septal loculi are lined with thin layers of fibro-lamellar calcite and are filled with pelletal carbonate sediment (pl. 2: 1a). The wall of the corallite has been removed by abrasion or solution, and the exterior of the corallite has been plastered with caliche that invades triangular areas cut into the septa.

A transverse thin section (EM 15159a; fig. 1c), cut near the top of the calice at an alar diameter of 10 mm, shows a short (1 mm), wedge-shaped cardinal septum and 19 longer (1.5–2.5 mm) wedge-shaped other major septa. Septa are preserved as calcite deposited in concentric layers parallel to the sides of the septa. No median dark lines are visible in the septa (see later discussion of "foundations of septa"). The epitheca is not preserved; the exterior is coated by dark, microcrystalline caliche that has invaded the outer parts of the septa. Alar and counter septa are not distinguishable, and minor septa are absent.

A longitudinal thin section (EM 15159d; fig. 1d; pl. 2: 1c) was cut in the cardinal-counter plane between transverse sections EM 15159b and c. The right side of the section intersects the loculus on one side of the cardinal septum, which is partly filled by sediment. The left side of the section cuts through the counter septum, which is silicified. The middle of the section cuts through the stereoplasmic filling of the axial region of the corallite. The concentric layers of stereoplasm visible in EM 15159b are defined by subparallel fine lines that are concave upward in the axial region (pl. 2: 1c). No tabulae are visible.

In summary, the holotype preserves only the ephebic stage of the corallite, a range in septal complement of 18–20. This stage is characterized by well-marked cardinal and counter septa, poorly-marked alar septa; and no minor septa. Although the floor of the calice is marked by a deep axial pit, suggesting the presence of an aulos, the originally open axial area produced by shortening of the major septa was filled in by stereoplasm during growth of the polyp. No tabulae are preserved in the axial region or in the peripheral region of this specimen.

←
 aulos of phyllotheca-type, $\times 15$, f early ephebic stage (axial stereoplasmic infilling and inner ends of major septa altered by silica not distinguished from open space), $\times 15$. 2. USNM 88138C: a early neanic stage, showing major septa of right quadrants free, except for stereoplasmic connections, $\times 15$; b, c early neanic stage, showing arrangement of major septa, $\times 15$; d early neanic stage comparable to figs. 1a–c, $\times 15$; e neanic stage, showing aulos of phyllotheca-type, $\times 15$; f ephebic stage, showing major septa radially arranged and almost equal in length, $\times 7.5$. 3. USNM 415746F, topotype: a–d early to late neanic stage, showing zaphrentoid arrangement of septa replaced by phyllotheca-type aulos, $\times 15$; e, f ephebic stage, $\times 7.5$. 4. USNM 140348 (illustrated by Stumm 1948: pl. 17: 26): a, b neanic stage, showing zaphrentoid arrangement of major septa, $\times 15$; c, d late neanic stage, showing recrystallization of axial area (white) that may have destroyed aulos of phyllotheca-type, $\times 15$; e ephebic stage, showing half-moon arrangement of layers of axial stereoplasm open toward counter septum, $\times 7.5$.

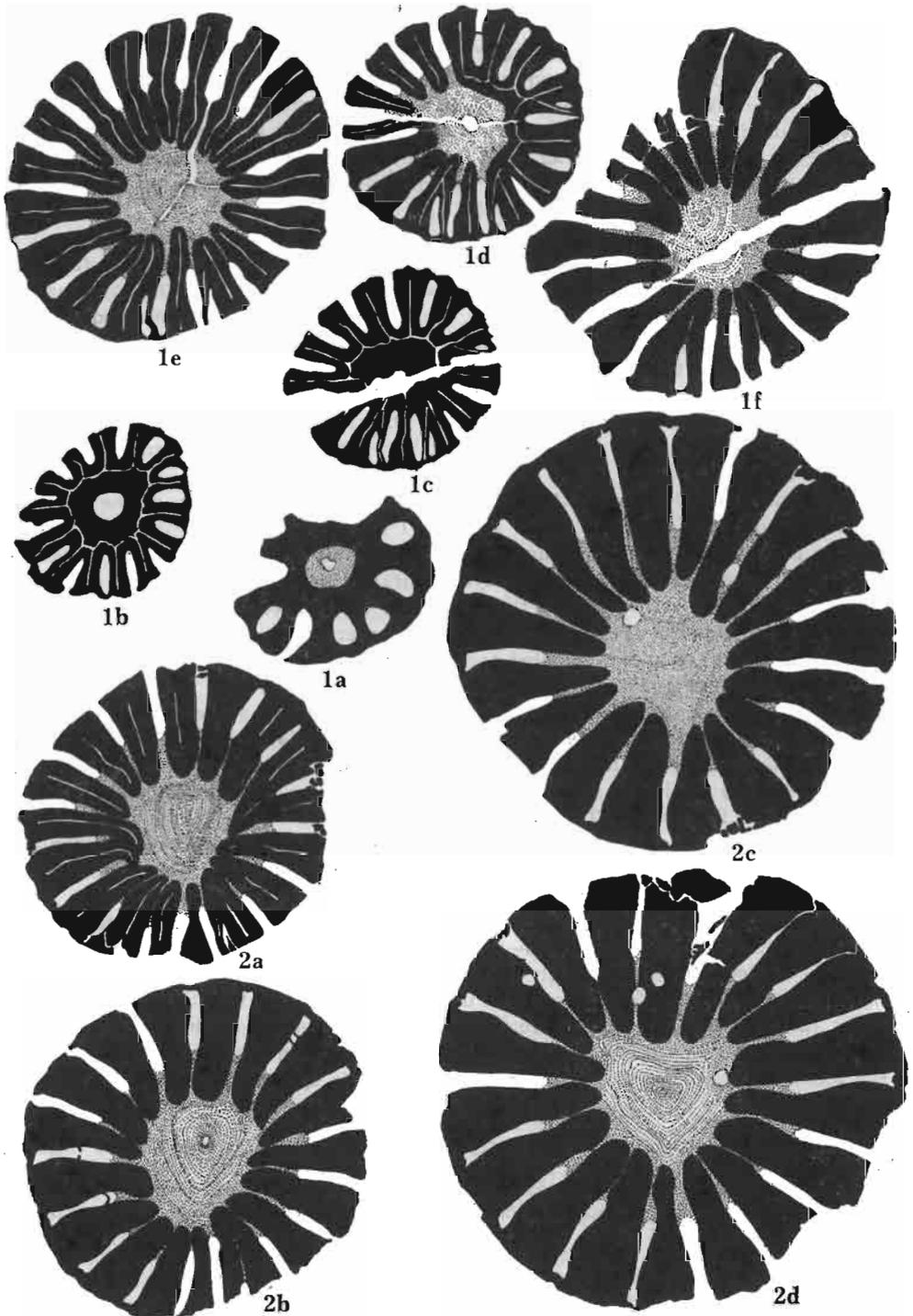


Fig. 4. *Trochophyllum verneuianum* Milne-Edwards and Haime, 1850. Transverse thin sections. 1. USNM 88112F: Corallite tending morphologically toward *Trochophyllum* sp. 1. a early neanic stage, showing early open aulos, $\times 15$; b neanic stage, showing all middle lines of primary septa united around open aulos, $\times 15$; c, d late neanic stage, showing some major septa in cardinal quadrants becoming discon-

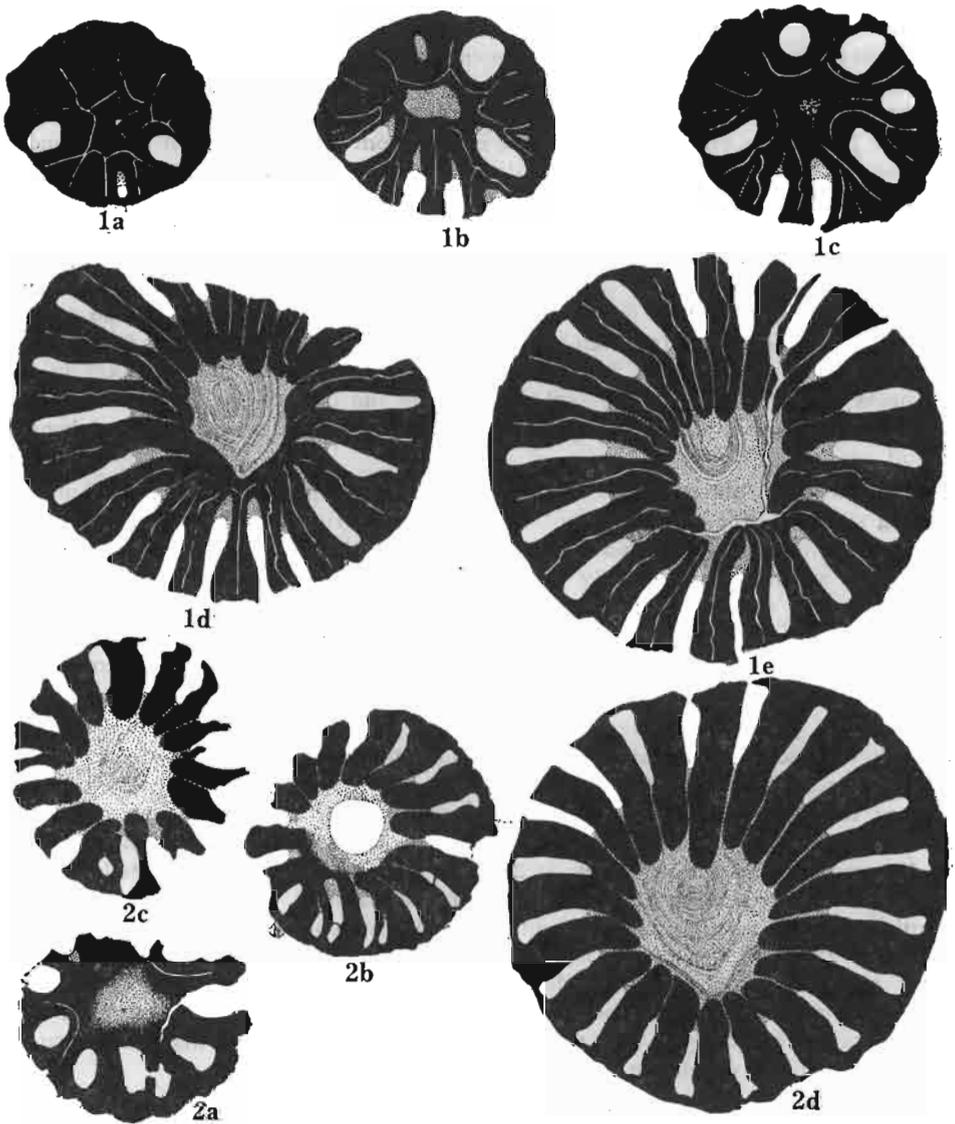


Fig. 5. *Trochophyllum verneuianum* Milne-Edwards and Haime, 1850. 1. USNM 415746G, topotype. a—c neanic stage showing zaphrentoid arrangement of septa $\times 15$; d ephebic stage; additional septal lamella is attached to inner end of cardinal septum, $\times 7.5$; e ephebic stage; cardinal septum is long but additional septal lamella disappeared, $\times 7.5$. 2. USNM 88112B. a—c neanic stage; a, b showing aulos filled in with stereoplasm $\times 15$; c showing aulos temporarily open $\times 15$; d ephebic stage showing cardinal septum slightly shortened and counter septum elongated a little $\times 7.5$.

nected while aulos remains open, $\times 15$; e, f—ephebic stage, showing axial area completely filled in with stereoplasm and slightly elongated cardinal and counter septa, $\times 7.5$. 2. USNM 415746R, topotype: a—d successive sections of early to late ephebic stage, showing concentric deposition of axial stereoplasm readily visible in most sections and waves of minor septa developed in some loculi, $\times 7.5$.

Individual variation in other specimens studied.—1. *The calice:* Because none of the specimens has the calice margin preserved, the presence of foundations of minor septa can only be inferred. The occurrence of septal waves (see Morphogenetic Interpretation) can be deduced easily from the presence of corresponding furrows on the exterior of the corallite. Nearly complete upper parts of calices of some specimens (pl. 1: 2a, b; pl. 4: 2a; pl. 6: 1a) having no traces of protuberances of the external wall toward the lumen indicate that these foundations must have been very shallow, if present at all, and must have disappeared very early by being overgrown by flatly-disposed layers of calcium carbonate during growth of the calice.

The arrangement and length of the major septa are variable and so are the width and shape of the free axial areas and calices themselves (pl. 1: 2b; pl. 4: 1a, 2a, 3; pl. 5: 1—5; pl. 6: 1a, 2a). Variation in development of the stereoplasm that connects the inner ends of the septa and covers the calice floor is also substantial. Thus, the calices are more variable than transverse sections made just beneath them.

The widely funnel-shaped, rather shallow and open calice of the holotype, having stereoplasmic connections of major septa restricted to the lower portions of the latter, must be considered typical, in spite of the fact that none of the other specimens studied shows exactly this morphology. Even the morphologically closest specimens (pl. 4: 1a; pl. 5: 1) are deeper in the axial portions and have stereoplasmic interseptal sheets developed higher in cardinal than in counter quadrants. The number of reasonably well preserved calices is limited, which limits conclusions that can be drawn from them.

All well preserved calices show the following characters in common; (1) Axial area free of septa surrounded by inner ends of major septa connected by stereoplasm. Stereoplasm forms the axial part of the calice floor, which is inclined upward toward the cardinal septum. Vertical interseptal infillings of the stereoplasm are always lower near the counter septum, sometimes with an additional depression at the counter septum itself (pl. 5: 2; pl. 6: 1a). (2) A shallow depression in the stereoplasm surrounding the inner end of the cardinal septum (homolog of the cardinal tabular fossula) or the fossula followed by deposition of stereoplasm (pl. 1: 2b; pl. 4: 2a; pl. 5: 3—5; pl. 6: 1a, 2a). (3) Major septa that have very thick foundations, rather thin and smooth blades, and slightly rhopaloid ends. The upper ridges of the major septa do not show any swellings that could be interpreted as large trabeculae. (4) No traces of minor septa or their foundations; they may have occurred at tops of calices, which are missing in the specimens studied.

The following variations have been established: (1) The axial area ranges from a narrow but rather shallow depression (pl. 5: 1) or a narrow pipe (pl. 4: 3; pl. 5: 2) through several intermediate kinds of depressions (pl. 1: 2b; pl. 4: 1a, 2a; pl. 5: 3, 5) to an axial platform that is broad and differentiated, but always higher near the cardinal septum (pl. 5: 4; pl. 6: 1a, 2a). (2) The mutual relation of inner ends of major septa and their relation to the stereoplasmic infillings depends in part on the width and shape of the free axial area of the calice. Where the area is very narrow, and especially where it is pipe-shaped, the major septa are semiradially or bilaterally arranged, with the symmetry axis formed by the cardinal and counter septa (pl. 4: 3; pl. 5: 5). This kind of arrangement can also be deduced from slightly broken calices (pl. 5: 3, 5). The inner ends of the major septa seem to be straight, at least for so long as they are recognizable in the stereoplasmic sheets of the calice floor. In some calices (pl. 1: 2a; pl. 6: 1a, 2a), however, the inner ends of the septa bend slightly toward the cardinal septum, or are arranged in a zaphrentoid-like plan (pl. 4: 2a). The tendency of the major septa to incline toward the cardinal septum is especially well seen in specimens having their axial areas comparatively wide and

shallow (pl. 6: 1a). All these specimens, as well as most of those having a narrow axial area, show the stereoplasmic infillings almost lacking near the counter septum, but connecting the inner ends of the major septa in the cardinal quadrants to almost half their height, thus forming a stereoplasmic wall inclined upward toward the cardinal septum (pl. 1: 2b; pl. 5: 3—5; pl. 6: 1a, 2a). (3) Length of the cardinal septum slightly variable, having its inner end invariably reaching the stereoplasmic wall of the aulos and commonly being almost equal to the other major septa. Very rarely, the cardinal septum is clearly shorter than the adjacent major septa in the calice (pl. 4: 2a), but even then the stereoplasm reaches it by forming a shallow depression in the aulos. The height of this septum (length in cross section through the calice) is much smaller than that of adjacent major septa, and it is almost invariably thinner, at least in its inner portion. The cardinal septum of the holotype is of the same kind, and its apparent shortening (pl. 1: 1a) resulted only from burial of its inner part in matrix. Also the length (or height) of its foundation, equal to that of other major septa, is confirmed by the thin section made near the top of the calice (fig. 1c). (4) Length and thickness of the counter septum, the counter lateral septa, and the alar septa. The counter septum may be slightly longer than counter lateral septa or even slightly elongated independently of other characteristics of the calice (pl. 1: 2b; pl. 4: 3). Most commonly, it is equal to the other major septa, although it may be slightly thicker than the counter lateral septa. The counter septum may appear elongated because of slight shortening of the counter lateral septa (pl. 5: 1). The latter septa, however, are most commonly equal to other major septa in length and thickness, like the alar septa.

2. *Morphology of mature growth stage and comparison to calice:* The following characters of the holotype seem most important for comparison with other specimens of the species: (1) the almost equal length of the major septa, except for the cardinal septum (slightly shorter) and the counter septum (slightly longer); (2) the slight inclination of most of the major septa toward the cardinal septum; (3) the complete infilling of the aulos with stereoplasm, whose concentric growth lines were probably related to the shape of the calice (pl. 2: 1b; pl. 3: 3; pl. 7: 1f; pl. 9: 1a, b). Although all the corallites investigated in detail and assigned to the species can be compared readily to the holotype, the whole set of holotype characters listed above is neither common nor constant within the collections.

The following individual variation was noted: (1) The arrangement and shape of major septa. In the great majority of specimens, the major septa are strongly dilated at the periphery (foundations), rather narrow in the middle parts, and somewhat rhopaloid within the inner zone of axial stereoplasm (pl. 3: 2f; pl. 7: 2d, 3e; pl. 9: 2, 2f; fig. 4: 1e, 2c, d). The cardinal and counter septa are straight, but the rest of the major septa bend more or less distinctly toward the cardinal septum, with the common exception of the counter lateral septa. This curvature of the major septa is differently accentuated in different coralla, being strong in the entire section (pl. 7: 2d; pl. 8: 3e), or hardly recognizable, except for some (fig. 3: 4e). The strongest inclination of the major septa toward the cardinal septum occurs during the early ephebic stage of most coralla. In some, however, the major septa are straight and radially disposed in this part and bent slightly toward the cardinal septum just beneath the calice floor (pl. 3: 2f). In contrast, some other coralla show strong curvature of the major septa in the late neanic/early ephebic stage prolonged up to the base of the calice, causing both connection of median lines of some septa (continuation of fragmentary phyllothea) and formation of separated septal bodies arranged perpendicular to septa and connected to their inner ends (pl. 7: 3e). No traces of these bodies occur in the wide and shallow, but otherwise typical, calice of this corallite (pl. 6: 1a). In parts of sections of some specimens, the major septa

are slightly narrower near the external wall (pl. 7: 1f; pl. 9: 1a, b; fig. 4: 2c, d), which is characteristic of *Trochophyllum* sp. 1. However, we were not able to check the earlier existence of foundations of minor septa in such loculi (see Morphogenetic Interpretation). A few small specimens (pl. 3: 1g, 2f; pl. 7: 1f; pl. 8: 1c), considered immature, show the irregularly radial arrangement of major septa similar to some immature portions of larger corallites.

(2) The configuration of the axial stereoplasm is probably a function of both the arrangement of major septa and the shape of the inner surface of the calice. The great majority of the corallites investigated show a clear lamination of the axial stereoplasm, with horseshoe-shaped traces of individual laminae in plan view, open toward the counter septum and counter lateral septa (pl. 7: 2d, 3e; pl. 8: 1c, 3c). In almost all calices of these corallites (illustrated and not illustrated) (pl. 1: 2b; pl. 4: 2a; pl. 5: 1, 4, 5; pl. 6: 1a, 2a), the stereoplasmic interseptal infillings are much higher near the cardinal than near the counter septum, and the latter is free almost to the calice floor. Also, the axial part of the calice floor (the aulos) is inclined, sometimes steeply, upward toward the cardinal septum on the convex side of the corallite. In some corallites, however, the horseshoe-plan of the axial stereoplasm is accompanied by a pipe-like shape of the axial part of the calice (pl. 4: 3), in which the interseptal stereoplasmic infillings are slightly higher near the cardinal septum. In other corallites (pl. 7: 1f), a temporarily concentric arrangement of the axial stereoplasmic laminae (pl. 7: 1f) is accompanied by an asymmetric calice.

3. *Protosepta*: This term is used herein in the traditional meaning, comprising the cardinal, counter, alar, and counter lateral septa. Among these six septa, the alars are unrecognizable in mature corallites, their positions being marked only by the points of insertion of new major septa in the counter quadrants.

The cross section of the cardinal septum varies both in length and thickness, especially in its peripheral part. In contrast to the holotype, it is commonly as long as the adjacent major septa (pl. 3: 2f; pl. 8: 1c; fig. 3: 2f) or, rarely, it may even be slightly longer in some growth stages in other specimens (pl. 7: 2d, 3e; fig. 3: 2f, 4e; fig. 4: 1e). This elongation is especially obvious near the level of insertion of new major septa in cardinal quadrants (pl. 7: 3e; fig. 3: 3f; fig. 4: 1e), although the cardinal septum may be shorter than the average (fig. 4: 1d). The shortening of the cardinal septum below the calice floor is never distinct, and it always reaches the aulos (pl. 5: 3, 5), which is related to the shape of the tabulae (see Morphogenetic Interpretation). Also, the elongation of this septum is only relative; it never penetrates the aulos. These small differences in the cardinal septum are not considered taxonomically important.

The counter septum and counter lateral septa generally form an easily recognizable unit that is a counterpart of the cardinal septum, marking the bilateral symmetry of the corallite. The counter septum is almost invariably straight, with the inner end directed toward the cardinal septum. It may be slightly thicker and/or longer than counter lateral septa, but it is most commonly equal to the latter. The counter lateral septa are commonly the first septa whose inner ends bend slightly toward the cardinal septum (pl. 7: 2d, 3e; pl. 8: 1c, 3c). However, they may be parallel to the counter septum or even slightly inclined toward it (pl. 7: 2d), although the latter is extremely rare within the collection.

4. *Minor septa*: Although the minor septal furrows are certainly present, no traces of true minor septa are present either in the lumen or in the microstructure of the external wall (pl. 3: 2d; pl. 9: 1b). Some corallites have low protuberances on the inner surface of the external wall, which may be either foundations of septa or simply septal waves (pl. 9: 1a, b) (see Morphogenetic Interpretation for further discussion).

5. *Ontogeny*: Although the earliest parts of corallites are missing in all specimens available for study, investigation of the proximal ends of some specimens (pl. 2: 2; pl. 3: 1a) and the broken tip of *Trochophyllum* sp. 1 (pl. 10: 1a) reveals the basic rugosan arrangement of major septa in the brephic stage. The entire septal apparatus consisted of the axial septum and two pairs of lateral septa (alar and counter lateral) directly connected by their median lines to the former. This primary arrangement of septa, containing some metasepta as well, can be found in some corallites of comparatively large dimensions (pl. 2: 2; pl. 7: 3a, b). It is not certain whether this structure is really primary because ontogenetically younger parts of these corallites are missing. In all specimens whose very early growth stages are preserved, this basic septal structure, rarely supplemented by a pair of first metasepta, is replaced by a primary aulos (pl. 3: 1b—d; pl. 7: 1a—d; fig. 3: 1a—c) whose morphology compares with the phyllotheca of Grabau (1922). This early aulos is almost invariably filled in with stereoplasm and never continues into the mature part of the corallite. It underwent different modifications, making the late and middle neanic stages quite variable. In some specimens, either immediately (pl. 3: 2a—e; fig. 3: 2a—c) or after some growth (pl. 3: 1e, f; fig. 3: 1d, e), the primary aulos is replaced by an arrangement of septa that can be called anti-zaphrentoid because the counter septum is separated from other major septa and is located in a counter septal fossula. This is the most common morphology of the growth stage discussed, and it can last for a long growth period in some corallites. It can be rearranged again into an aulos comparable to the phyllotheca (pl. 3: 1f) or to the stereotheca (all mature corallites) of Grabau (1922) (see Morphogenetic Interpretation, p. 28, for further discussion).

In some corallites (pl. 7: 1a—f), the anti-zaphrentoid arrangement of major septa does not appear, or it is camouflaged by the circumaxial position of united major septa (pl. 8: 1a, b). The major septa may also be arranged in such a way that the cardinal septum, not the counter septum, is free (fig. 4: 1c, d) and forms the keystone of the aulos. Moreover the origin of the zaphrentoid and anti-zaphrentoid morphology is slightly variable. The variation discussed is significant, but we consider it intraspecific because individual variants were found in different combinations during ontogeny of individual corallites.

6. *Microstructure*: Superficially, the inner morphology of the septa is strongly influenced by both the extraordinarily large foundations of septa and the well laminated secondary sheets of septa. Commonly, the strong recrystallization invariably observed in the material studied tends to follow growth lines of these two elements, destroying very thin and delicate peripheral parts of primary septa, and causing the septa to appear as inner thickened parts of these sheets (pl. 11: 1a).

Closer examination, in transverse thin sections, of peripheral parts of some naturally coloured septa (pl. 11: 1c, d) documents a substantial difference in the morphology of both lateral *versus* axial and peripheral *versus* inner parts of the septa. The growth lines at the periphery may be dome-like (pl. 11: 1c) but narrow inwards to form a solid, dark middle line (see Morphogenetic Interpretation).

We have no direct data concerning the manifestations of trabeculae in the calice, where inner ridges of septa are smooth when preserved. Also, in spite of many trials, we were unable to prepare a well oriented longitudinal section, perhaps because the primary septa are very thin. An oblique thin section (pl. 11: 1b) does not clearly confirm the occurrence of trabeculae.

Transverse thin sections of septa (pl. 12: 1—4), although not adequately preserved to be conclusive, permit elimination of lamellar microstructure in the primary septa *sensu* Schindewolf (1942). The absence of this microstructure is indicated by the direct contact of inner parts of the primary septa (pl. 12: 3), by the preserv-

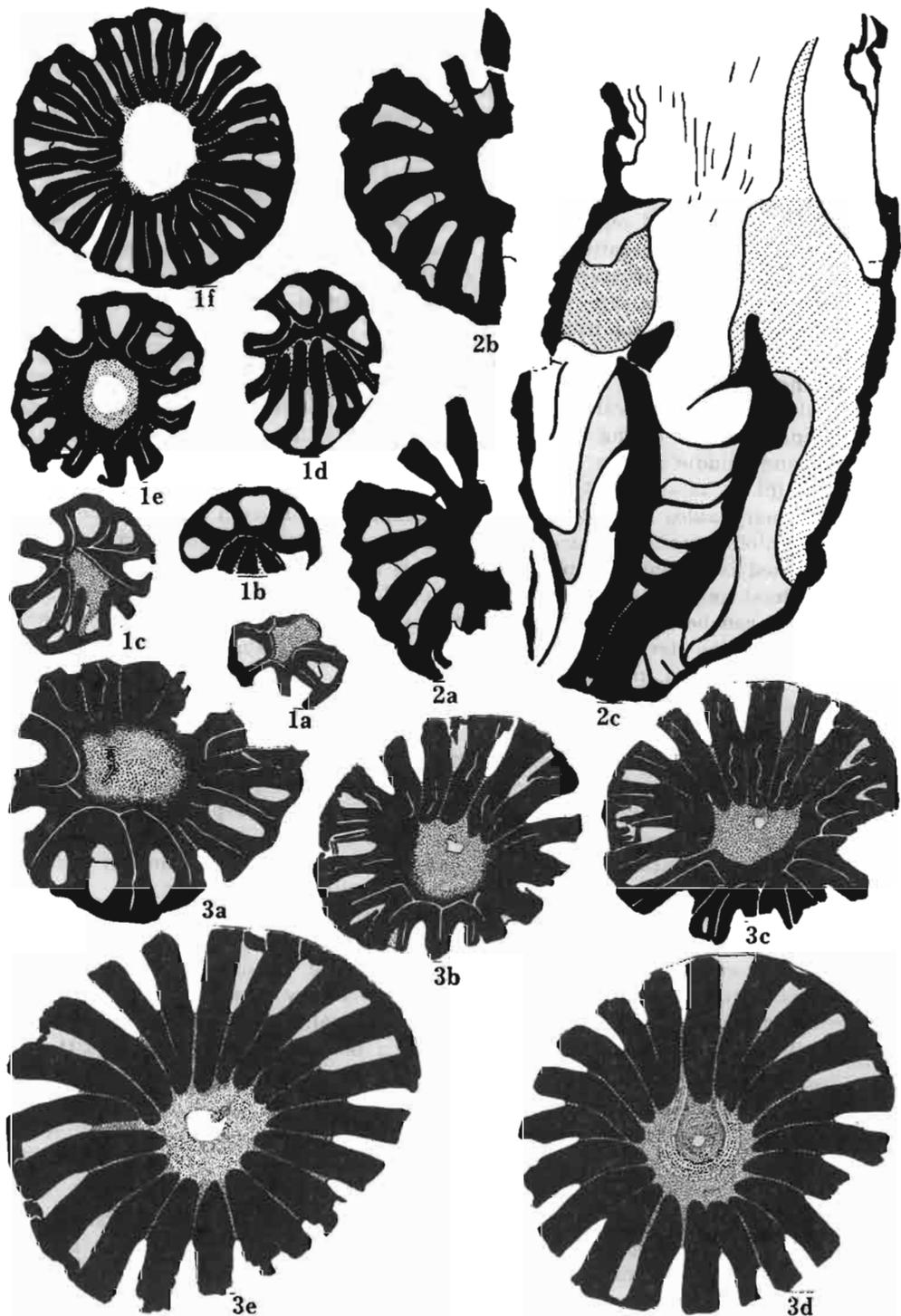


Fig. 6. *Trochophyllum* sp. 1. 1. USNM 37459A, transverse thin sections: a early neanic stage, showing well developed aulos filled in with stereoplasm, $\times 15$; b—d neanic stage, showing disappearance of aulos and rearrangement of minor septa into zaphrentoid plan and length of cardinal septum varying through growth, $\times 15$; e late neanic/early epebic stage, showing aulos supplemented by a septal body

ed morphology of the latter, and by configuration of growth lines of secondary sheets of septa, which are parallel to the primary septum (pl. 11: 1c). The two remaining possible microstructures are fibro-normal and trabecular (or diffuso-trabecular *sensu* Kato 1963). The diffusion of dark dots (pl. 12: 1, 2) in the inner and middle parts of the primary septa favors the second possibility. Diagenetic alteration of a solid, fibro-normal microstructure to produce the observed structure seems rather doubtful to us, and we consider this structure trabecular, although we were not able to document the centripetal arrangement of crystals within individual dark dots. The same is true for the peripheral parts of better preserved septa (pl. 12: 4), where the dark dots are larger than in the septal parts discussed above. In conclusion, we consider the microstructure of the primary septa to be fine trabecular or diffuso-trabecular, whereas the septal foundations and the secondary stereoplasmic sheets of septa are lamellar.

Trochophyllum sp. 1

(pls. 1, 2, 5, 6, 9, 10, 12; figs. 6, 7)

Material studied.—USNM 37459A, E, F; 415746D, G, H, K, L, O; 415747A—E; 8 sectioned and 6 unsectioned corallites. All specimens are partly silicified. Some have calices and/or most parts of proximal ends preserved.

Diagnosis.—*Trochophyllum* having n:d ratio as much as 20:8.4 at calice margin; aulos without complete stereoplasmic infilling; tabulae well developed; foundations of major septa present from early maturity on.

Description of typical specimen.—Although no holotype was chosen, we describe one typical corallite in detail and compare others to it for establishing intraspecific variation. USNM 415747A was chosen for detailed description because it has a fairly well preserved calice and tabularium. It shows two shallow rejuvenations in its middle growth stage and in the calice.

Removal of matrix from the calice (pl. 6: 4a) revealed slight shortening of the cardinal septum and a counter septum equal to counter lateral septa. The lengths of the alar septa are uncertain because the calice is rejuvenated and slightly flattened near their positions. This lateral rejuvenation involves most or all of the cardinal quadrants, being deepest near the cardinal septum. Only very low parts of the septa in the calice are connected by stereoplasm. There are no minor septa at the calice margin, but their foundations are well developed (pl. 6: 4a).

A transverse thin section made just beneath the floor of the calice (fig. 6: 1e—g) confirms the slight shortening of the cardinal septum and the equality of the counter septum to counter lateral septa. The alar septa are unrecognizable by length and thickness. All major septa are radially disposed, with two to three pairs adjacent to the cardinal septum having their inner ends bent slightly aside of it. Peripheral parts of all major septa are barrel-shaped, i.e., narrowing both near the

located next to cardinal septum, $\times 15$; f ephebic stage, $\times 7.5$. 2. USNM 37459F: a, b two successive transverse thin sections of half of longitudinally broken corallite, $\times 7.5$; c longitudinally broken corallite, $\times 7.5$. 3. USNM 415746O, transverse thin sections: a late neanic stage, showing uncertain relation of septa to axial stereoplasmic infilling but no open aulos, $\times 15$; b, c late neanic/early ephebic stage, showing slightly open aulos and ambiguous relation of axial stereoplasm to inner ends of major septa in some parts, $\times 7.5$; d, e ephebic stage, showing small opening of aulos and other characters intermediate toward *T. verneuilanum*, $\times 7.5$.

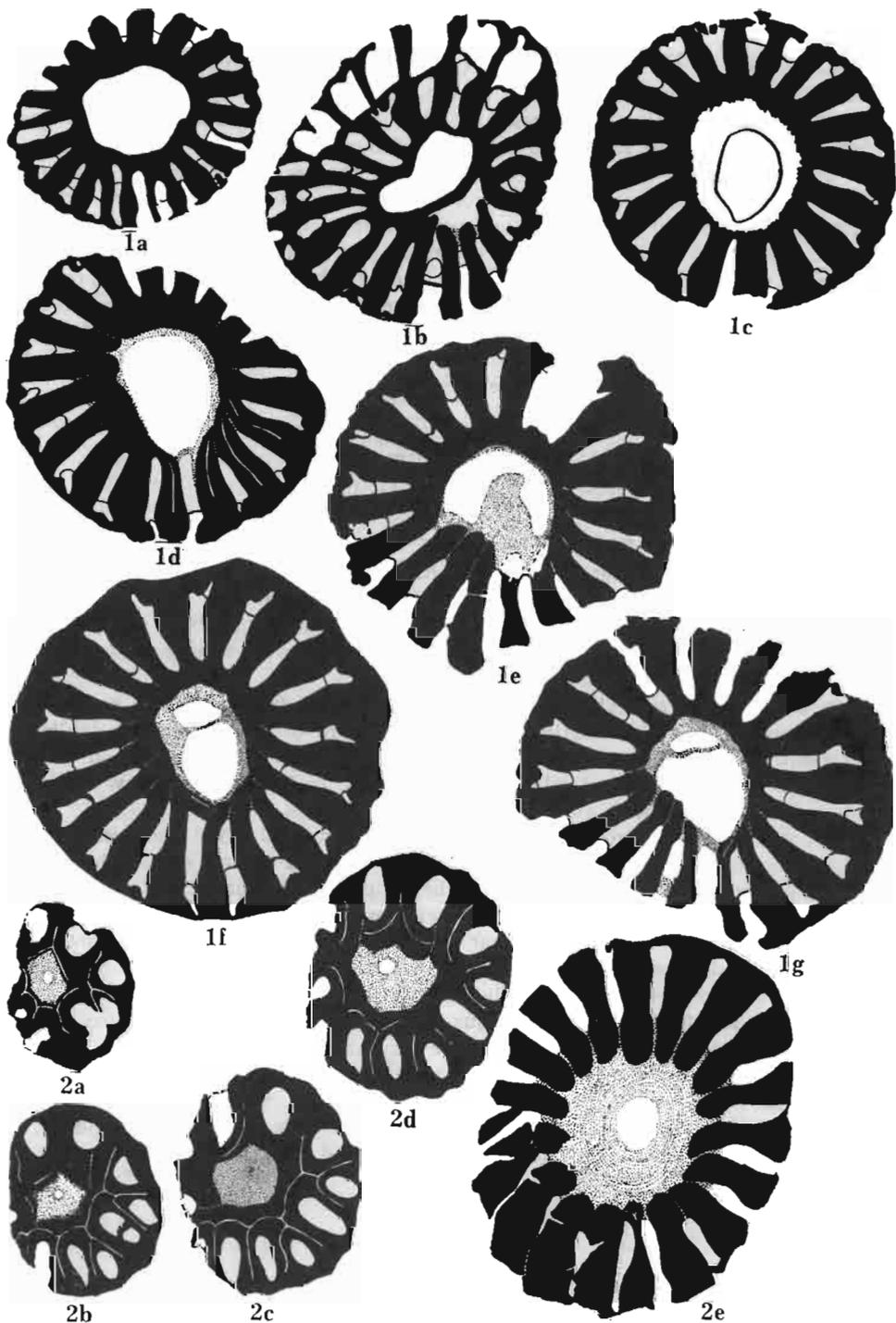


Fig. 7. *Trochophyllum* sp. 1. 1. USNM 415747A, successive transverse thin sections: a early ephebic stage; b lateral rejuvenation of counter quadrants; c, d ephebic stage, showing uncertain relationship of inner ends of septa to stereoplastic ring in aulos (white in 1c); e ephebic stage, showing section partly through axial part of tabula; f, g ephebic stage. All $\times 7.5$. 2. USNM 415746H, successive transverse thin

external wall and toward the aulos. Their inner ends are only slightly thickened, but median lines of some are united. A solid and continuous ring of stereoplasm surrounds the inner ends of major septa inside the otherwise empty aulos.

Foundations of minor septa are well developed in the form of solid knobs located closer to the cardinal side of each major septum (fig. 6: 1c—g). The counter septum is thus easily recognizable by having two of these foundations attached closely to it. Sections of some tabulae, obliquely attached to the foundations of some minor septa on one side and to adjacent major septa on the other, indicate the possible presence of an incipient biform tabularium (fig. 6: 1d, left). More inwardly-located tabulae are normal.

Rejuvenation that occurred in the middle growth stage of the corallite was rather shallow and did not cause any significant morphological changes, except for the development of an almost complete new external wall (fig. 3: 1b). Also, the ontogenetically youngest preserved part of the corallite (early ephebic, fig. 6: 1a) shows a morphology similar to that described above.

The longitudinally-broken corallite (pl. 1: 3; fig. 5: 2c), although slightly flattened in the uppermost part, shows well the morphology of different growth stages in longitudinal view. The ontogenetically youngest part of the corallite is characterized by an almost solid axial stereocolumn, whose basal origin is confirmed by the occurrence of a single, well-defined axial part of the lowermost tabula. The axial stereocolumn changes into an open aulos by widening of the diameter of the stereocolumn and reduction of inner stereoplasm.

The tabularium is bipartite. Peripheral parts of tabulae are arranged steeply upwards and tend to be clearly S-shaped, with peripheral edges attached perpendicularly to the external wall. Inner edges of peripheral parts of the tabulae penetrate the wall of the aulos and merge with this wall, confirming the basal origin of interseptal parts of the aulos and the continuity of inner and peripheral parts of the tabulae as well. No peripheral tabellae were observed, but axial tabellae are present inside the aulos, indicated by both the number of axial *versus* peripheral basal structural elements and by their mutual relations. The shape and thickness of axial tabellae are similar to the corresponding parts of the tabulae. Peripheral rejuvenation (fig. 5: 2c, left) does not disturb the morphology of the tabularium described.

Individual variation in other specimens studied.—1. *Ontogeny*: Only one of the corallites included here has a nearly complete early ontogeny preserved. The primary zaphrentoid distribution of major septa (pl. 10: 1a) was replaced by a temporary primary aulos (pl. 10: 1b; fig. 5: 1a) that was transferred into the deformed zaphrentoid arrangement. A small area devoid of stereoplasm appeared only in the higher part of the aulos (pl. 10: 1c—e; fig. 5: 1d); the rest of the axial area is filled with stereoplasm. The empty aulos that appeared next is a typical phyllothea built from the inner ends of major septa, which are deflected toward each other and joined by their median lines in some specimens (pl. 10: 1f; fig. 5: 1e). This ontogeny is very similar to that of most of the specimens of *T. verneuillanum* except for the empty aulos in the neanic stage.

The early ontogeny of two other specimens investigated in detail differs from that described above in the persistent occurrence of the phyllothea from the

← sections: a—d early to late neanic stage, showing change in morphology of aulos from bordered directly by primary septa (2a), through uncertain relation of those two structures (2b), to phyllothea with most primary septa united by middle lines and temporary disappearance of axial opening of aulos, $\times 15$; e ephebic stage, showing slightly elongated cardinal and counter septa, $\times 7.5$.

earliest stage of growth studied (pl. 9: 3a—e; fig. 2a—d). However, the tips are missing in both these specimens, and both have the aulos completely filled in with stereoplasm in some early ontogenetic sections. USNM 415746H illustrates well a possible occurrence of two keystones in the ontogeny of the aulos, where the cardinal and counter septa produced an additional septal lamella to complete the aulos (especially fig. 6: 2), but only the cardinal septum retained that role to maturity (fig. 6: 2e). The ontogeny of USNM 41576D, which has primary septa that are short and very clearly united along the entire part of the early ontogeny studied (pl. 9: 3a—d), differs in these respects from all coralla of both *T. verneuianum* and *T. sp. 1* studied in detail.

2. *Calice and morphology of mature growth stage*: All calices are either flattened and filled in with matrix or destroyed. Some preserved parts (not illustrated) do not show any significant differences from the above description, at least in marginal portions. Moreover, the morphology below calices (pl. 9: 3e; pl. 10: 1g, 2d; fig. 5: 1f, g, 2e) is rather uniform, with small differences concerning more wedge-shaped peripheral parts of septa (fig. 5: 3e; pl. 6: 2e) and a possible absence of foundations of minor septa. This is only an inference, however, because the external wall is lacking in these specimens. The same corallite, as well as USNM 415746D (pl. 9: 3e), shows no traces of tabulae in the transverse thin section, which one of us (JF) considers the result of diagenesis. This is not the rule for specimens from the same locality as the holotype of *T. verneuianum* because some of them (USNM 415746K, L) have the tabulae well-developed. However, in both these specimens, the aulos is temporarily filled in with stereoplasm, which makes these portions very similar to *T. verneuianum*.

Discussion.—The group of specimens described above is distinguished from *T. verneuianum* mainly by having an empty aulos, much better development of foundation of minor septa in most corallites, and the presence of tabulae. However, the first two characters vary in some specimens and the third, or rather its absence, may have been caused by diagenesis. Also, the slightly smaller dimensions are closely comparable to some corallites of unquestionable *T. verneuianum* morphology. These considerations and the fact that the specimens were not collected bed-by-bed are the main reasons for not introducing a formal new name for this group of specimens. They are very obviously related to *T. verneuianum*, but we do not consider them conspecific.

The obviously close morphological similarity of these specimens to *Neaxon* Kullman, 1965 and especially to *Neaxonella* Weyer, 1978 is discussed in remarks on the genus. We consider *Trochophyllum* to be related to *Neaxon* and *Neaxonella*, but we do not consider these genera as synonyms.

MORPHOGENETIC INTERPRETATION

Growth of septa in calice

The remarks that follow concern mainly the minor septa. We do not attempt to solve the problem of the taxonomic value of the presence or absence of these septa in the Rugosa, restricting ourselves to those aspects of the problem that relate to specimens studied for this paper.

According to Hill (1981: F35), the septum is the "radially disposed longitudinal portion of the corallite". We would add to this short definition that this "portion of corallite" was secreted in an ectodermal pocket

characterized by a specific histology, which we consider important for further discussion. One of us (Fedorowski 1974, 1986a) maintains that data concerning the occurrence of so-called "lamellar microstructure" of septa (Schindewolf 1942) are not convincing. Hence, only two main kinds of septal microstructure exist in the *Rugosa*: trabecular and fibro-normal. The fibro-normal microstructure seems to be only a modification of the trabecular type and resulted from a very close arrangement of centers of calcium carbonate crystallization.

Peripheral parts of the septa in *Trochophyllum* do not show either of the two basic kinds of microstructure, exhibiting a distinct lamination instead. This lamination can extend for quite long portions of the septa in individual corallites, but is hardly recognizable in others. Similar structures, observed in many other genera, always appear at the calice ridge and are transformed into trabecular or fibro-normal septa during their further growth toward the calice interior. Fedorowski (1986b, 1987) called these structures "foundations of septa". The material studied in this paper shows that there are structures even more primitive than the foundations of septa. The latter structures were interpreted as being inserted in septal pockets, which were too wide to permit trabecular or fibro-normal histology. They extended deeper into the calice interior than could be explained by a simple waviness of the calcite margins due to longitudinal septal ribbing. On the other hand, the most primitive homologue of septa, or the introductory step of their appearance, was the direct result of the

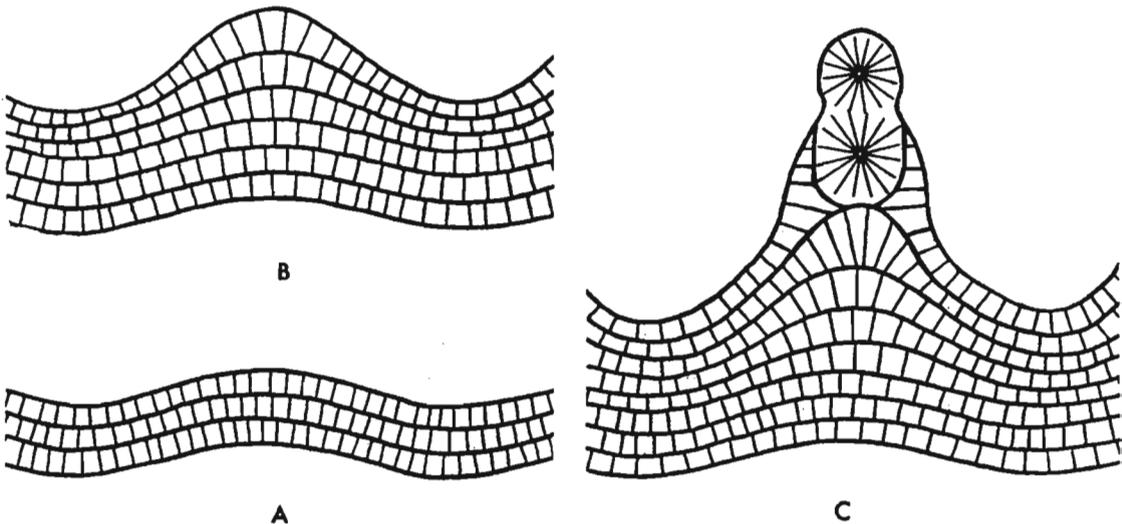


Fig. 8. Reconstruction of three predicted steps in formation of septa as seen in transverse section. a septal wave corresponding to septal furrow, without reconstruction of growth lines of external wall, b foundation of septum, showing additional septal thickening, following septal wave, causing distinct protuberation inside calice but no formation of true septal pocket; c primary septum, formed in septal pocket following two preceding steps (basal stereoplasmic sheets may cover its lateral surface) (not to any scale).

waviness mentioned. Their growth lines are simply growth lines of the external wall. We thus propose to call these structures "septal waves" (fig. 7a). *Trochophyllum* may be an example of a genus having these structures developed instead of true minor septa.

The rugose coral genera that have both septal furrows as well as major and minor septa well developed show three steps of minor septal development: (1) Septal waves, in which the growth lines follow exactly the waviness of septal furrows (fig. 7a); (2) Foundations of septa, characterized by the growth lines penetrating the calice interior deeper than caused by the arch of peripheral depressions of septal furrows (fig. 7b). These lines, although commonly symmetrical on both sides of the septal foundation, do not show the structure called "median line of septum"; (3) Septa: "radially disposed longitudinal portions of corallites" (Hill 1981: F35), having the median lines developed (fig. 7c). The histology of these lines (= primary septa of Schouppé and Stacul 1955, 1959) may differ or may be discontinuous, but calcite fibers either form trabeculae or are directed in the cross section at a more or less constant angle of 180 degrees on both sides of the symmetry axes of the lines.

Minor septa in almost all better preserved specimens of the collection studied either stopped at the level of septal waves (*T. verneuilanum*) or formed, at most, the foundations of septa (*Trochophyllum* sp. 1). Even in corallites having these structures developed best (pl. 6: 4a; pl. 10: 2c, d), they do not have median lines developed. Thus, we consider that true minor septa are absent in *Trochophyllum*, although underdeveloped homologs are present.

The major septa went through all three of the steps described above in their development. The long stage of development of foundations of septa, characteristic of the genus, is illustrated by strong thickenings of peripheral parts of septa composed of conical growth lines (pl. 2: 1a; pl. 8: 3c; pl. 11: 1a, c, d). Some of these septum-like bodies seem not to develop a normal septal histology almost to their periaxial portions, being formed mostly from narrow cones of calcium carbonate sheets (pl. 8: 3c). This morphology would thus fit the definition of the lamellar microstructure of Schindewolf (1942). They were obviously inserted in deep septal pockets and acted as septa, but are considered foundations of septa in this paper (see below, for further discussion).

In many specimens, both the foundations of septa and the true septa are covered by secondary, basal (*sensu* Schouppé and Stacul 1955, 1959) stereoplasmic sheets. These sheets follow the initial shape of septa and their foundations (fig. 7c), but many camouflage that original shape as well (pl. 8: 1c; pl. 9: 1a, b; pl. 10: 1g; fig. 4: 2b—d; fig. 5: 1b, 2a; fig. 6: 1c—g, 2e).

Comparatively numerous major septa, especially in *Trochophyllum* sp. 1, have their peripheral-most portions narrowed by comparison to the

strongly thickened adjacent portions (pl. 7: 1f; pl. 8: 1c). These peripheral narrowings are most commonly accompanied by foundations of minor septa. We interpret the cause of this phenomenon as the lack of space in peripheral portions of septal loculi for the first lateral expansions of secondary sheets of septa. Tending to retain some space in its external parts, the polyp may have created a mechanism preventing the immediate contact of pockets of major and minor septa or their foundations. In some corallites, or in parts of them, a barrel-like shape of major septa is seen, although no traces of foundations of minor septa are evident in the given loculi. We interpret these as remnants of the earlier coexistence of both septal structures. In wedge-shaped peripheral parts of major septa, the foundations of minor septa were not observed. Thus, the lateral thickening of the former was not disturbed.

Deposition of axial stereoplasm in mature portions of corallite

Investigation of well preserved specimens of *Trochophyllum* sp. 1 and of some fragments of specimens of *T. verneuillanum* permit the following interpretation of insertion of the axial, periaxial, and interseptal stereoplasm. Inner parts of tabulae and their shape form the basis for that insertion, at least in early stages of corallite growth, with the possible

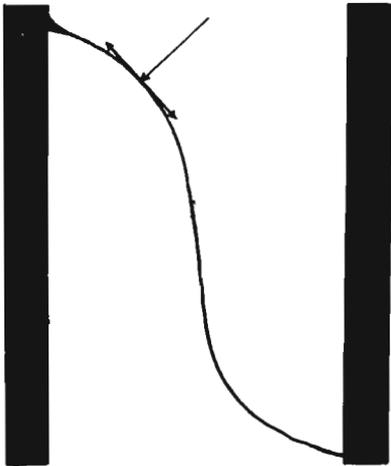


Fig. 9. Reconstruction of longitudinal section of tabula attached to stereocolumn (left) and external wall (right); arrows show distribution of stress produced by polyp body on most convex part of tabula.

exception of the primary aulos. The stereoplasmic sheets are restricted exclusively to major septa and to the axial and periaxial parts of the tabularium. Peripheral portions of tabulae are very thin and easily destroyed by postmortem diagenesis. The stability of the construction formed by very thick and strong major septa and strong axial portions, invariably present in all specimens of both species, prove their genetic determination. We are presently unable to find a reasonable explanation

for the origin of that structure. The occurrence of very delicate peripheral parts of tabulae may well have been purely mechanically determined. The polyp, hanging on the strong framework of axial and radial skeletal elements, needed only a weak support for its peripheral part, especially when its pressure on the peripheral parts of tabulae was divided into two vectors directed toward the strong axial column and the peripheral wall, which was greatly strengthened by thick septal foundations (fig. 9). This is clearly proven by the shape of peripheral parts of the tabulae, which are not only steep, as in a Gothic ceiling, but are also S-shaped, making their structure even stronger due to the mechanical strength created by their shape (pl. 1: 3; fig. 5: 2c).

The arrangement of the tabulae and, consequently, the arrangement of stereoplasm, was determined by the horn-shape of the corallite and by the position of the cardinal septum on the convex side of the corallum. This caused a seemingly higher position of the cardinal part of the calice, which is obvious when the calice ridge is compared to the curvature of the corallite. The calice ridge is always almost perpendicular to the curvature of the corallite. However, because of the curvature, the peripheral parts of individual tabulae must be slightly taller on the convex than on the concave side of the corallite, resulting in an oblique calice floor. This obliqueness, especially well seen in the axial part of many calices (pl. 1: 2b; pl. 4: 2a; pl. 5: 2, 4; pl. 6: 1a, 2a), was caused by declination of those parts of tabulae toward the cardinal quadrants.

Tabulae were most probably complete, i.e. not divided into axial and periaxial tabellae (fig. 10a, b), at least in the absence of the cyathotheca (= axial coil of Hill, 1981: F32). True axial tabellae may occur, but only

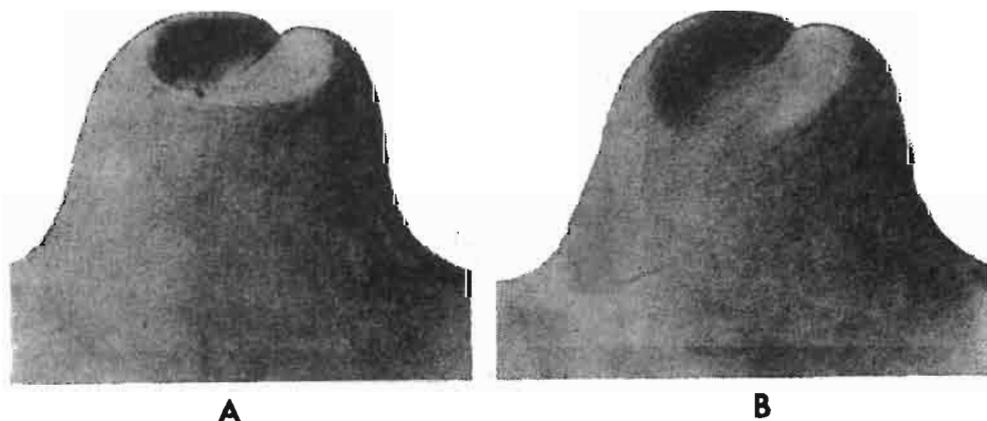


Fig. 10. Reconstruction of two tabulae in *T. verneuilanum* with major septa removed. A tabula that forms pipe-like axial part of calice (cf. pls. 4: 3, pl. 5: 2); strong stereoplasmic ring in its uppermost part, located between inner ends of major septa, forming boundary of aulos, depression of cardinal fossula (up) is not always so well developed as shown here; B tabula having its cardinal part more distinct and protruded higher than counter part (cf. pls. 5: 4, pl. 6: 1a, 2a). Drawn by Rafal Wojciechowski, M. Sci.

as additional structural elements (see remarks on longitudinal section). The periaxial, highly inclined parts of the always complete tabulae (between the ends of major septa), bend strongly downward to form the flat and oblique axial portions. These strongly bent parts of tabulae, having an everted U-shape, are always strengthened by stereoplasm because they are mechanically the most critical parts for support of the polyp body. The occurrence of such a bend in the tabulae is detectable also in complete stereoplasmic infillings of the axial parts of corallites, the holotype included (pl. 2: 1c).

As shown by the depression in the periaxial stereoplasm, invariably present in all calices studied, a cardinal tabular fossula is present in *Trochophyllum*. Its function, like the function of the aulos, must have been related to the water vascular system within the gastrovascular cavity of the polyp.

Observations of specimens having the aulos empty proves our supposition that the stereoplasm was inserted on surfaces of tabulae, but its growth between the inner ends of the septa was almost continuous. Thus, direct observations of these parts of the tabulae is very difficult, commonly impossible, because there was almost no sudden shifting of the polyp body causing its disconnection from the basal skeleton. Lack of space between the adjacent of calcium carbonate layers is the only difference between such a structure and separate tabulae because both were inserted by exactly the same part of the basal disc of the polyp. Thus, we cannot see any substantial difference between the origin of these two kinds of biogenic deposits, except for direction of growth, which is centripetal just below the newly up-shifted body (Wells 1969, Sorauf 1972) and simply upward after completion of the tabula, as when sudden body-shifting did not take place.

The same is true of the complete infiling of the aulos where, in a sense, there are not tabulae because there was not sudden body-shifting and no separation between the individual basal layers of the stereoplasm. One might describe the solidly infilled aulos of *Trochophyllum* as being occupied by a single, very thick tabula. In auloses where interruptions were observed (pl. 7: 1a—f; fig. 4: 1a—f, 2a—c; fig. 5: 2c; fig. 6: 2a—e), the number of tabulae would thus correspond to the number of interruptions. We were not able to correlate these interruptions with peripheral tabulae because the latter are missing, but such a correlation is highly probable, although the number of peripheral portions of tabulae do not necessarily correspond to the number of axial breaks in stereoplasmic deposition. Increase in the axial stereoplasmic column may have been continuous, while the thin, peripheral positions of tabulae were built in a normal, cyclic way.

The absence of tabulae in the peripheral portions of most corallites of *T. verneuillanum* resulted either from destruction during postmortem

diagenesis (JF) or they were developed and then resorbed by the polyp and obliterated before burial of the corallite (WJS). The lack of recognizable separate tabulae in the axial stereocolumn of this species resulted from continuous deposition in the manner described above.

Origin of aulos and early morphology of calice

The earliest stage of the aulos, most commonly beginning at the stage of six protosepta, was comparable to the cyathotheca (see Description). The comparison is not completely certain because Grabau's (1922: 19—22) original description of the cyathotheca did not specify: (a) whether the median lines of septa (= primary septa) were united, (b) the origin and arrangement of the secondary sheets, and (c) whether the inner area of the aulos was filled in with stereoplasm or how the latter originated, if present.

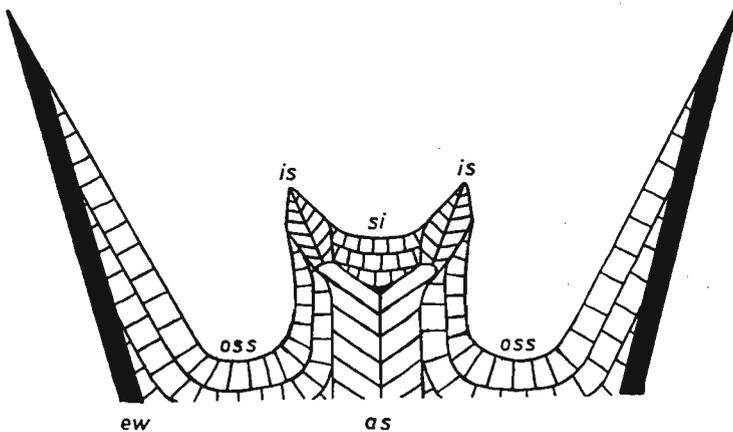


Fig. 11. Reconstruction of early stage of development of aulos in *T. verneuilanum* as seen in longitudinal section perpendicular to axial septum; *as* axial septum; *ew* external wall; *is* inner ends of primary septa inserted to cessation of growth of middle part of axial septum; *oss* outer stereoplasmic sheets covering external wall, basal plate, and axial septum, and expanded on newly inserted major septum; *si* stereoplasmic infilling of aulos.

Our studies of *Trochophyllum* strongly suggest that the primary aulos originated by an axial splitting of protosepta that formed the primary septal apparatus in the brephic stage (pl. 3: 1a; pl. 7: 1a; pl. 10: 1a). The term "axial splitting" is a descriptive term based on study of thin sections. The primary aulos formed at the beginning as a kind of slit elongated in the cardinal-counter plane (pl. 3: 1a, b; pl. 7: 1a; pl. 10: 1b). The slit is filled in with stereoplasm and is surrounded by primary septa, i.e., by the apparently naked, directly united median lines of the protosepta. Each of these protosepta has its peripheral, centripetally arranged

portion covered on both sides by secondary stereoplasmic sheets. Each is seemingly divided into two circumaural forks that are convex toward the aulos. These forks are common for two adjacent septa without any traces of the middle keystone and are covered peripherally by the secondary sheets of stereoplasm that continuously surround both lateral sides of radial portions of two septa facing to the same septal loculus and the outer side of their common circumaural part. The inner side of that common part of a primary septum is not covered by the secondary sheets of stereoplasm. The stereoplasm is developed inside the primary aulos, but the arrangement of calcium carbonate crystals there is perpendicular to that in the primary septa, similar to the tabulae and the secretions of the basal disc.

The appearance of the "axial splitting" of the protosepta revealed by the structure of the septal apparatus and of the axial stereoplasm does not literally mean splitting of these septa, especially the axial septum, along their symmetry axes, but this appearance does illustrate changes in polyp morphology. Obviously, the primary arrangement of protosepta, which were directly united during the brephic stage, could have originated only in the axial fold of ectoderm (axial septum), having lateral digitations in which the alar and counter lateral septa were formed. We believe that the primary fold originated from the basal disc of the young polyp and then expanded toward the calice margin. This deduction is purely conjectural, derived from the fact that the primary protosepta were directly united, a conclusion not confirmed by studies of very young calices, which are not present in the collection. Some observations by Fedorowski (1987), made on other genera and families, indirectly confirm this interpretation.

The primary aulos, i.e., the apparent "axial splitting" of the primary septum, originated from a cessation of the upward and inward growth of the axial portions of these septa and, especially, of the axial septum. Because of this cessation of growth, as well as the smoothing and flattening of the middle part of the axial fold of the basal disc in which the protosepta of the brephic stage were inserted, the axial septum was divided into cardinal and counter septa, and the radial arrangement of the other protosepta began.

Observations of the weathered tips of corallites and the morphology of the earliest ontogenetic stages investigated in thin sections indicate that the primary septal apparatus grew upward during some period of the brephic stage. Hence, the primary septal loculi were able to reach as much as 1—2 mm in depth before the primary aulos originated. Such an arrangement of the polyp body and the skeleton, which were much higher in their axial parts, influenced the increase in stereoplasm observed. The growth of the stereoplasm was not changed in the peripheral parts of septal pockets, i.e., those surrounding the six primary

septal loculi. Only the shape of the inner portions of the latter was changed, but they remained as closed as they were before the aulos was inserted.

The axial parts of the polyp and skeleton were totally rearranged. These parts were highly uplifted owing to earlier growth and later influenced the shape of peripheral parts of tabulae, where tabulae formed. The original axial slit, which originated by cessation of growth of the axial portion of the uplifted calice floor (upper ridges of the united protosepta), was very narrow and increased in width, approaching a more or less circular shape simultaneously with corallite growth. The widening inner area of the aulos, covered with a flat part of the polyp basal disc, was contemporaneously filled in with stereoplasm, which grew upward, i.e., perpendicular to the ectoderm. Deposition of axial stereoplasm followed the growth of the inner arches of septa bordering the aulos so quickly that the secondary stereoplasmic sheets were not able to develop on their inner, periaular sides. Thus, only the primary septa were present there, while the secondary sheets continued to develop on their outer surfaces, facing in to the deep interseptal loculi (fig. 11).

We are not certain that the primary aulos, described and interpreted above, was developed in all specimens of the genus. Most probably, it was present, at least in a partial form, during an episodic time span (pl. 10: 1b). An apparent of that structure may have resulted from diagenetic alteration, or it was simply missing because the earliest stage studied was too advanced to capture this feature.

As mentioned in the descriptive part of the paper, the morphology of corallites, and thus morphogenesis, changed during the middle and late neanic stage. The ontogeny of USNM 415746C (pl. 3: 1a—g; fig. 3: 1a—f) is one of the reasons for considering these significant differences as intraspecific variations. Following the stage of primary aulos (pl. 3: 1a—d; fig. 3: 1a—c), this specimen developed a deformed zaphrentoid morphology (pl. 3: 1e; fig. 3: 1d), which appeared probably as a result of almost complete infilling of the primary aulos with stereoplasm and of reorganization of folds of ectoderm in such a way that completely separated septal pockets of most of the major septa appeared (pl. 3: 1e; fig. 3: 1d). These separate pockets almost meet at the calice axis and come very close to the pockets in which the united septa continued to increase (pl. 3: 1f; fig. 3: 1e). However, both the separated and the united septa were now covered with secondary sheets inside and outside the aulos, although remnants of the latter (a simple axial pit in this stage) were continuously folded in with the axis stereoplasm. The slower increase of that stereoplasm left time for the complete development of stereoplasmic sheets on both sides of the septa.

The deformed zaphrentoid morphology was again replaced by an aulos (pl. 3: 1f; fig. 3: 1e) filled in with stereoplasm, but the morphology of the

new aulos differed from that of the primary aulos because the primary septa were then covered with secondary sheets of stereoplasm on both their inner and outer sides. The primary septa only reached the lateral sides of secondary stereoplasmic sheets of adjacent major septa, but the median lines of the primary septa did not meet. Such morphology is closely comparable to zaphrentoid or anti-zaphrentoid in the sense of a separation of some septal pockets and their elevation above the flat axial disc, which allowed deposition of both primary septa and their secondary sheets. The reorganization of inner portions of those pockets into circumaxial position in the aulos is the only difference. The primary counter septum or keystone of the new structure, seems to be divided in its inner part into two forks (pl. 3: 1f; fig. 3: 1e). The additional fork of that septum is a supplementary septal lamella that appeared in the additional fold of the ectoderm. The origin of such lamellae was discussed in detail by Schouppé and Stacul (1959) and Fedorowski (1986).

The connection of the additional lamella described above with the inner end of the counter septum is well illustrated by some thin sections of USNM 88138B (pl. 7: 3b—e). In successive sections, the septum seems to bend in opposite directions, being supplemented on the other side by the lamella mentioned above. Such an instability resulted from the inconstant upward growth of the counter septum, which had two alternating regions of growth interruption located on the edge of the aulos on both sides of the counter septum. The temporary separation of the left or right lamella depended on the actual activity of one of these lamellae. The ontogenetically youngest preserved part of this specimen illustrates clearly an anti-zaphrentoid arrangement of the major septa (pl. 7: 3a).

In contrast to the specimen discussed above, the major septa of some corallites (e.g., USNM 140348, fig. 3: 4a, b) do not meet axially, leaving a more or less wide axial area filled in with stereoplasm. Also, the ontogenetically older sections of USNM 104348 do not show a cyathotheca, and we would rather homologize that morphology with the stereocolumn or at most with the phyllotheca. Because the proximal end of the corallite was ground down by Stumm (1948) without thin sections or camera lucida drawings being made, we can only infer that the primary aulos was developed during that earlier part of growth. The inner ends of major septa, slightly inclined toward each other at the ontogenetically youngest preserved part of growth, may provide indirect proof of our conjecture. The morphology described was possibly due to the straightening and successive flattening of inner ends of septal pockets when the basal upgrowth of the stereoplasm started to prevail. The insertion of new major septa made that morphology similar to the zaphrentoid type. The increase in axial stereoplasm formed the main difference between the morphology discussed and the stereocolumn on the one hand and the stereotheca on the other. In the stereotheca, the increase in stereoplasm

is restricted to lateral parts of inner ends of septa and to the interseptal loculi in the circumaxial area, while the axial tube remains empty; *Trochophyllum* sp. 1 illustrates this well. In the stereocolumn, however, the complete infilling of the axial tube is caused by rapid upgrowth of the stereoplasm that replaces normal tabulae, and the inner ends of major septa "disappear" in the axial stereoplasmic mass. A stage of separation of these septal ends depends on the elevation of inner ends of septal pockets, but it may have been camouflaged by postmortem diagenetic alteration (fig. 3: 4c, d).

The morphogenetic differences between the stereocolumn and stereothea are rather insignificant. Their diagnostic value cannot be excluded, however, if these characters are constant, as in *Trochophyllum*, where we arbitrarily consider them adequate for species identification.

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JERZY FEDOROWSKI i WILLIAM J. SANDO

MORFOGENEZA I POKREWIEŃSTWA *TROCHOPHYLLUM* MILNE-EDWARDS
ET HAIME, 1850 (COELENTERATA, ANTHOZOA)*Streszczenie*

Rewizja rodzaju *Trochophyllum* Milne-Edwards et Haime, 1850, przeprowadzona na podstawie przebadanego ponownie holotypu gatunku typowego *T. verneuillianum* Milne-Edwards et Haime, 1850, licznych topotypów i innych okazów pochodzących z tego samego poziomu stratygraficznego w Kentucky, USA wykazała, iż rodzaj ten jest zapewne endemitem ograniczonym do basenu środkowoamerykańskiego. Oprócz gatunku typowego, cechującego się dużą zmiennością wewnątrzgatunkową, wydzielono jeden gatunek pozostawiony w nomenklaturze otwartej.

Trochophyllum cechuje się skomplikowaną ontogenezą, w której można wyróżnić stadium aulusu pierwotnego i fyllocjatoteki, wypełnionej steroplazmą i tworzącej kolumnę osiową; trabekularną mikrostrukturą septów pierwotnych, osłoniętych wtórnymi pokrywami o mikrostrukturze lamellarnej; płytką fossulą główną; oraz otwarciem aulusu ku septum przeciwległemu, które stanowi zwornik systemu.

Na podstawie analizy morfogenetycznej poszczególnych stadiów rozwojowych i elementów strukturalnych ustalono, iż różnice w depozycji zwartej stereoplazmatycznej kolumny osiowej i cienkich tabul peryferycznych mogą wynikać z czysto mechanicznego rozkładu obciążeń, chociaż ich stałość świadczy o genetycznym zakodowaniu tych cech. Nieciągłość w osiowej części kolumny stereoplazmatycznej jest dowodem na to, iż zarówno tabule, jak i kolumna mają identyczną genezę. Tylko stopień intensywności depozycji węglanu wapnia lub okresowo szybszy wzrost osiowej części koralita, powodujący oderwanie się jego dysku bazalnego i wytworzenie szkieletu z przerwą równą rozstępowi pomiędzy tabulami, stanowią różnice pomiędzy tymi elementami.

EXPLANATION OF PLATES 1—12

All photographs by E. Chwieduk, M. Sci., except where noted.

Plate 1

Trochophyllum verneuillianum Milne-Edwards and Haime, 1850

1. EM 15159, holotype. External characters. *a* calice, $\times 6$, *b* cardinal side, $\times 4$, *c* counter side, $\times 4$, *d* alar side, $\times 4$. Photographs by K. R. Moore.

Trochophyllum sp. 1

2. USNM 4157460. *a* upper part of external wall enlarged to show growth striae and lack of septal furrows, $\times 10$; *b* calice, showing slight elongation of counter septum and depression of cardinal fossula in highly protruded cardinal part of aulos, and low and thin cardinal septum reaching limit of aulos, $\times 6$.
3. USNM 37459F, longitudinally broken. Empty, thick-walled aulos protruded high in calice; axial parts of tabulae horizontal, slightly sagging; peripheral tabulae S-shaped, steeply declined toward aulos, $\times 8$.

Plate 2

Trochophyllum verneuianum Milne-Edwards and Haime, 1850

1. EM 15159, holotype. *a* portion of transverse thin section "b", showing bipartite morphology of major septa well accentuated by union of peripheral growth lines of stereoplasmic sheets of adjacent major septa; *b* portion of transverse thin section "b", showing relation of axial stereocolumn to inner ends of major septa; *c* portion of longitudinal thin section "d", showing axial stereocolumn. All $\times 30$, photographs by K. R. Moore.
2. USNM 415746B, topotype: broken tip showing zaphrentoid arrangement of septa retained up to comparatively wide diameter of corallite, $\times 20$.

Trochophyllum sp. 1

3. USNM 37459F; transverse thin section of half of broken specimen (for longitudinal section, see pl. 1: 3), showing waves of minor septa and peripheral parts of tabulae well developed, $\times 10$.

Plate 3

Trochophyllum verneuianum Milne-Edwards and Haime, 1850

Transverse thin sections

1. USNM 415746C, topotype: *a* surface of broken tip, showing arrangement of major septa around aulos, which is filled in with stereoplasm, $\times 20$; *b-d* early neanic stage, showing "dark lines" of major septa directly contacting stereoplasmic infilling of aulos, $\times 20$; *e* early neanic stage, showing temporary disappearance of aulos and rearrangement of septa into zaphrentoid morphology, $\times 20$; *f* neanic stage, showing reappearance of aulos filled in with stereoplasm, attachment of inner end of counter septum to lateral, secondary sheet of left counter-lateral septum, and additional septal plate between counter septum and right counter-lateral septum, $\times 20$; *g* early epebic stage, $\times 10$.
2. USNM 88138C: *a-c* early neanic stage, showing zaphrentoid arrangement of major septa and axial stereocolumn varying in width from section to section, $\times 20$; *d, e* neanic stage, showing aulos filled in with stereoplasm and comprised mostly of bent and connected inner ends of major septa, some of which are straight, $\times 20$; *f* epebic stage, $\times 10$.
3. Specimen EM 15159, holotype: epebic stage, $\times 10$. Photograph by K. R. Moore.

Plate 4

Trochophyllum verneuianum Milne-Edwards and Haime, 1850

1. USNM 140348B: a calice, $\times 6$; b alar view (Stumm 1948: pl. 17: 26), showing external wall mostly eroded, $\times 4$.
2. USNM 415746B topotype: a calice, showing cardinal septum much thinner and slightly shortened in upper part of calice and counter septum equal to adjacent major septa, $\times 6$; b alar view, showing well preserved external wall with septal furrows, growth striae, bands of growth striae, and some shallow lateral rejuvenation, $\times 4$.
3. USNM 88112E: partly broken calice, showing deep, pipe-like aulos; cardinal septum thinner than other major septa and reaching aulos; elongated counter septum; and hole of worm tube near calice floor; $\times 6$.

Plate 5

Trochophyllum verneuianum Milne-Edwards and Haime, 1850

1. USNM 88138A: calice, showing cardinal septum slightly shortened and almost all major septa free, surrounding narrow, open axial area, $\times 6$.
2. USNM 37459C: partly damaged calice, showing counter and counter-lateral septa elongated and free, and aulos deep, fairly narrow, and pipe-like, $\times 4$.
3. USNM 88112F: calice, showing clear depression of cardinal fossula in aulos that is much higher in cardinal quadrants and cardinal septum that is much thinner and lesser in upward extent than adjacent major septa, $\times 4$.
4. USNM 88112H: calice, showing wide aulos that is much higher near barely distinguishable cardinal septum and counter septum, and some adjacent major septa free down to calice floor, $\times 6$.
5. USNM 88112G: calice, showing morphology similar to fig. 4, except for narrow, pipe-like aulos, $\times 4$.
6. USNM 415746G, topotype: cardinal view, showing corroded external wall but deep imprints of growth striae visible on septa, $\times 4$.

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7. USNM 415746H: alar view, showing imprints of growth striae on peripheral parts of major septa, $\times 4$.
8. USNM 37459A: cardinal view, showing imprints of growth striae on peripheral parts of minor septa and shallow rejuvenation, $\times 4$.

Plate 6

Trochophyllum verneuianum Milne-Edwards and Haime, 1850

1. USNM 88138B: a calice, showing cardinal septum thinner and less protruded than adjacent major septa, reaching small depression of cardinal fossula in wide aulos and free counter septum, $\times 6$; b alar view, showing delicate growth striae and very shallow septal furrows preserved in area most protected against corrosion, $\times 4$.

2. USNM 415746A, topotype: *a* calice, showing thin and low cardinal septum reaching distinct cardinal fossular depression in wide aulos that increases in height toward cardinal septum, $\times 6$; *b* cardinal view, showing corroded external wall, $\times 4$.
3. USNM 88138C: alar view, showing *in vivo* damage of middle part of corallite causing temporary narrowing of its diameter and damaged portion replaced by regular pattern of growth striae and septal furrows when repaired, $\times 4$.

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4. USNM 415747A: *a* calice, showing deep, laterally-axial rejuvenation, slightly damaged (cardinal septum right), $\times 6$; *b* exterior, showing deep septal furrows, growth striae, and shallow rejuvenations, $\times 6$.

Plate 7

Trochophyllum verneuilanum Milne-Edwards and Haime, 1850

Transverse thin sections

1. USNM 415746A, topotype: *a*—*c* neanic stage, showing aulos filled in with stereoplasm and bordered by "dark lines" of major septa whose inner ends are bent toward and united with adjacent septa, $\times 20$; *d*, *e* neanic stage, showing small opening temporarily developed in corallite axis, $\times 20$; *f*—early ephebic stage, showing radial arrangement of septa, $\times 10$.
2. USNM 415746E, topotype: *a*—*c* neanic stage, showing irregular aulos completely filled in with stereoplasm and built of major septa, only some of whose inner ends are united, $\times 20$; *d* ephebic stage, showing bilateral symmetry caused by inclination toward slightly shortened cardinal septum by all major septa except counter septum (note section of tabula in one of the left cardinal quadrant septal loculi), $\times 10$.
3. USNM 88138B: *a*—*d* early to late neanic stage showing anti-zaphrentoid arrangement of major septa whose direct connection by middle lines disappeared during growth (note variegated inclination of inner end of counter septum), $\times 20$; *e* ephebic stage, showing long cardinal septum, several major septa in cardinal quadrants either bent toward cardinal septum or produced circum-axial lamellae, and half-moon arrangement of axial stereoplasm open toward counter and counter-lateral septa, $\times 10$.

Plate 8

Trochophyllum verneuilanum Milne-Edwards and Haime, 1850

Transverse thin sections

1. USNM 88138A: *a*, *b* neanic stage, showing anti-zaphrentoid arrangement of major septa, with counter septum in "pseudofossula", $\times 20$; *c* ephebic stage, $\times 10$.
2. USNM 37459C: late neanic stage.
3. USNM 415746Q, topotype: *a* late neanic stage, showing anti-zaphrentoid ar-

rangement of major septa, with counter septum in counter "pseudofossula", $\times 10$; b, c ephebic stage, showing shortened cardinal septum and temporarily elongated counter septum (3b), $\times 10$.

Plate 9

Trochophyllum verneuillanum Milne-Edwards and Haime, 1850

1. USNM 415746R: a, b transverse thin sections, ephebic stage, showing small protrusion of external wall imitating minor septa in some septal loculi, $\times 10$.
2. USNM 415746N, topotype. Transverse thin sections: a, b, neanic stage, $\times 20$; c late neanic/early ephebic stage, showing small, temporary opening in the axial stereoplasm, $\times 10$.

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3. USNM 415746D. Transverse thin sections: a—d neanic stage, showing aulos filled in with stereoplasm at beginning and then starting to open, $\times 20$; e ephebic stage, showing empty part of aulos surrounded by wide ring of stereoplasm, $\times 10$.

Plate 10

Trochophyllum sp. 1

1. USNM 37459A: a broken tip, showing zaphrentoid arrangement of major septa, $\times 20$; b early neanic stage, showing aulos of phyllothea-type filled in with stereoplasm, $\times 20$; c—e neanic stage, showing zaphrentoid arrangement of septa, $\times 20$; f late neanic/early ephebic stage, showing opening of axial part of aulos, $\times 20$; g ephebic stage, showing radial arrangement of major septa that reach aulos without having their inner ends covered by axial stereoplasm, $\times 10$.
2. USNM 415746O: a neanic stage, showing aulos of phyllothea-type completely filled in with stereoplasm, $\times 20$; b early ephebic stage, showing appearance of axial opening in stereoplasmic column, $\times 10$; c, d ephebic stage, showing variable length of cardinal septum and arrangement of stereoplasm in aulos, $\times 10$.

Plate 11

Trochophyllum verneuillanum Milne-Edwards and Haime, 1850

Specimen USNM 37459D

1. a transverse thin section showing arrangement of growth lines of foundation of major septum, $\times 100$; b longitudinally-oblique thin section through middle part of major septum, showing bodies interpreted as trabeculae, $\times 100$; c, d transverse thin section "a", showing peripheral parts of two major septa having conical growth lines of foundations of major septa transferred into primary septa interpreted as being built of small, densely packed trabeculae and some secondary sheets of septa well marked in left picture due to natural colouring, $\times 100$.

Plate 12

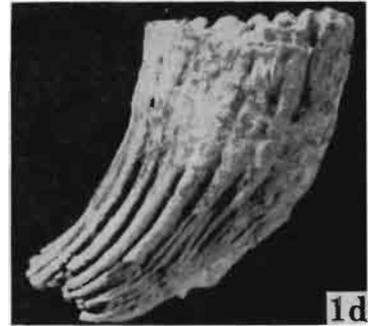
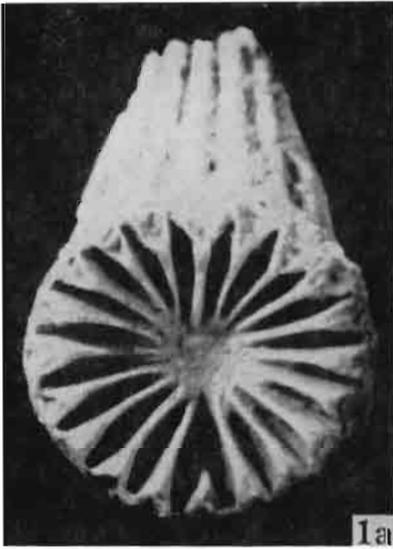
Trochophyllum verneuilanum Milne-Edwards and Haime, 1850

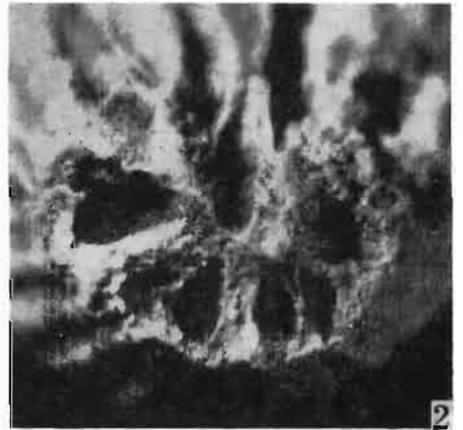
Transverse thin sections

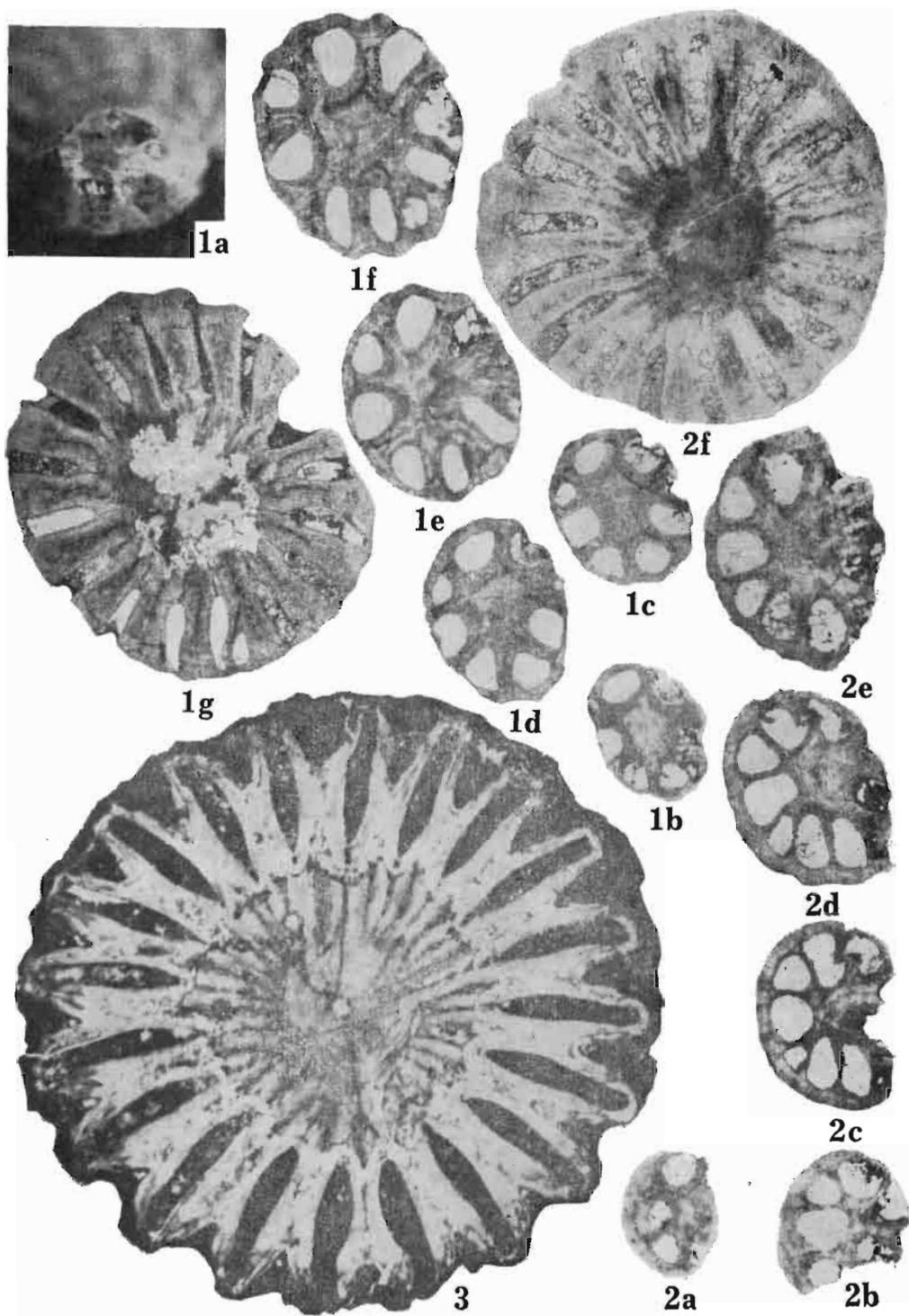
1. USNM 415746C, thin section "e", topotype: small, densely packed trabeculae in "dark line" of middle part of major septum, $\times 200$.
2. USNM 88112E, thin section "c": scattered multitrabecular morphology of inner part of septum (secondary sheets of stereoplasm better seen in left and top part of picture), $\times 100$.
3. USNM 88138C, thin section "f": early replacement of foundation of septum in external wall by trabecular microstructure of primary septum, $\times 100$.

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4. USNM 4157460, thin section "a": early growth stage, showing fragment of phyllothea-type aulos and section of very thin peripheral tabula in septal loculus, $\times 100$.









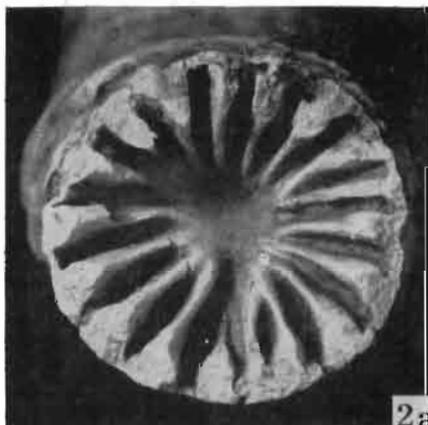
1a



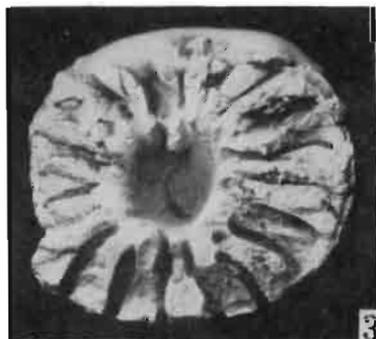
1b



2b



2a



3

