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A REVISION OF THE AULACOPHYLLOID TETRACORAL GENUS ODONTOPHYLLUM

BY ERWIN C. STUMM



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A REVISION OF THE AULACOPHYLLOID TETRACORAL GENUS ODONTOPHYLLUM

By ERWIN C. STUMM

AULACOPHYLLOID tetracorals, which are present only in strata of Middle Devonian age, possess such distinctive external and internal structures that they must be regarded as a cognate group. In members of this group the coralla always are simple and range from ceratoid to trochoid to patelloid and always have a pronounced curvature. The calyxes may be deep or shallow, and the calyx margins may be erect or have a peripheral platform.

The major distinctive external structure of the group is the quadrantal arrangement of the septa, which is clearly shown in the calyxes. The four protosepta are always easily distinguished. The cardinal septum lies in a deep fossula located on the convex side of the corallum. In some genera of the group the cardinal septum is short, but in others it extends from the wall to the axis. The alar septa are elevated above their neighbors, and the counter septum is elevated, elongated, or depressed in a small counter fossula. This arrangement of the protosepta divides the calyx into four quadrants. When the corallum is oriented with the cardinal fossula upward, the quadrants between the cardinal fossula and the alar septa are termed the left and right cardinal quadrants, and those between the counter septum and the alar septa the left and right counter quadrants.

The septa in the cardinal quadrants of most species are longer than those in the counter quadrants, which causes the axis to be subcentral and closer to the concave side of the corallum. These septa are directed pinnately toward the cardinal fossula at angles averaging 30 degrees. As a result of this arrangement, the septa in these quadrants have a distinct pinnate or herringbone pattern. The septa in the counter quadrants are parallel to the counter septum and are directed obliquely against the counter sides of the alar septa at

angles averaging 30 degrees. This structure gives the septa in the counter quadrants the appearance of radial symmetry and produces pseudofossulae on the counter side of the alar septa.

These structures are an illustration of Kunth's law of tetracoral septal insertion, but in no other group is it so conspicuous and so well shown in mature coralla.

The internal structures of the aulacophylloid corals are also distinctive and appear to be constant for the group as a whole. In the brephic and early neanic stages the septa in all four quadrants are greatly dilated and are in contact. Their quadrantal arrangement is very pronounced. In the later neanic stage the septa in the counter quadrants become attenuate, whereas those in the cardinal quadrants remain dilated. At this point dissepiments begin to appear between the septa in the counter quadrants. In some genera, such as Papiliophyllum, and in several species of Aulacophyllum this condition persists into the ephebic stage, and the dilated septa can be seen in the cardinal quadrants in the calyxes of mature individuals. In other forms, such as the genus Odontophyllum, and in Aulacophyllum sulcatum, the genotype species of Aulacophyllum, the septa in the cardinal quadrants become attenuate just as the ephebic stage is reached and dissepiments appear between them. In some genera such as Papiliophyllum and Eurekaphyllum a lonsdaleioid dissepimentarium is developed. Serial sections of Papiliophyllum show that this structure appears first in the counter quadrants during the early neanic stage. The septa in these quadrants are separated from the periphery, and the resulting space is filled with dissepiments. At the late neanic stage the septa in the cardinal quadrants begin to attenuate at their peripheral ends and then to withdraw from the periphery while retaining their dilation in their central and axial parts. The lonsdaleioid dissepimentarium is not fully developed around the cardinal quadrants until the beginning of the ephebic stage.

These structures present an unusual case of ontogenetic development. The cardinal quadrants are usually larger, and the septa in them are usually longer and invariably more numerous than those in the counter quadrants. In four typical specimens of *Odontophyllum convergens* (Hall) the septa in the cardinal quadrants range

from twenty-eight in the smallest specimen to thirty-eight in the largest, while those in the counter quadrants range from twenty-four in the smallest to thirty in the largest. The convex cardinal sides of the coralla are from two to three times the length of the concave counter sides. Nevertheless, the developmental stages always appear first in the counter quadrants.

Numerous investigators of the tetracorals have used the term "acceleration" to designate advanced structures in the cardinal or counter quadrants. Use of this term has been based largely on external features such as the number of septa. On this basis one would conclude that the cardinal quadrants of *Odontophyllum* are accelerated, which would be misleading. The use of such a term should be based on the development of the internal structures of the corallum as shown by serial tranverse sections.

Longitudinal sections of several species within this group show that the tabulae first appear in the early neanic stage and that in most forms they are incomplete, closely set, and distally arched. In some species they are broken up into small, distally arched tabellae. In only one species, *Eurekaphyllum breviseptatum* Stumm, are they complete and widely spaced. This undoubtedly is due to the short septa developed in this species. Dissepiments are present in all forms. They are the latest structures to form, always appearing first between the septa of the counter quadrants.

The following six genera are included in the aulacophylloid group: Aulacophyllum, Pinnatophyllum (?—Aulacophyllum), Hallia, Odontophyllum, Papiliophyllum, and Eurekaphyllum.

Of these the genus Odontophyllum is distinctive in that it possesses carinate septa and very low, broad, strongly curved patelloid coralla. So far as known, the genus is confined to strata of lower Ludlowville age, species occurring in the Beechwood limestone of southern Indiana and northern Kentucky and in the coral bed of the Hungry Hollow formation of southwestern Ontario. Because of their distinctive appearance and ease in recognition, species of Odontophyllum made excellent index fossils for strata of this age.

The remainder of this paper is concerned with the redescription of the known species of *Odontophyllum*.

SYSTEMATIC DESCRIPTIONS GENUS ODONTOPHYLLUM SIMPSON

Odontophyllum, Simpson, 1900, p. 210. Genotype.—By original designation, Aulacophyllum convergens Hall, 1882, p. 22; 1883, p. 281, pl. 17, figs. 1-2; 1884, p. 426.

Generic description.—Simple, short, strongly curved patelloid tetracorals having a concentrically annulated epitheca and a wide, shallow calyx with gently sloping walls. A peripheral platform may be present. The cardinal septum is on the convex side of the corallum and lies in a long, narrow, deep fossula. The remaining septa in the cardinal quadrants are directed pinnately toward this fossula. The alar septa are elevated, and the septa in the counter quadrants, which are directed obliquely toward them, create alar pseudofossulae. The counter septum may be slightly elevated or slightly elongated or both. No counter fossula is present. The septa are carinate with very short, vertically directed carinae, which project above the distal surfaces of the septa and give them denticulate distal edges. The tabulae are closely set, incomplete, and distally arched. In some specimens they may be broken up into small, distally arched tabellae. Dissepiments are present in the later growth stages.

Odontophyllum convergens (Hall)

(Pl. 1, Figs. 1-14; Pl. 2, Figs. 7-9)

Aulacophyllum convergens Hall, 1882, p. 22.

Aulacophyllum convergens Hall, 1883, pp. 281-282, pl. 17, figs. 1-2.

Aulacophyllum convergens Hall, 1884, p. 426.

Cyathophyllum tornatum Davis partim, 1887, pl. 80, fig. 1; non pl. 86, figs. 7-11.

Heliophyllum convergens Greene, 1903, p. 139, pl. 40, figs. 7-13.

Non Odontophyllum convergens Stewart, 1938, p. 31, pl. 5, figs. 4-6.

Description.—The coralla are small, rapidly expanding patelloid cones so strongly curved that their proximal points extend laterally beyond the calyxes. Specimens range from 25 to 45 mm. in diameter at the calyx, from 35 to 50 mm. in length on the convex side, and from 10 to 20 mm. on the concave side. In only a few specimens is the epitheca preserved, but in these it is thick and closely annulated, almost completely obscuring the peripheral edges of the septa. The calyxes are broad and shallow, with very gently sloping

walls. A narrow peripheral platform is present in most specimens above the concave side of the corallum. The cardinal quadrants are longer than the counter ones, which causes the axis to be subcentrally located nearer the margin of the calyx above the concave side of the corallum.

The septa show a distinct tetrameral arrangement. The cardinal septum is depressed and lies in a long, narrow fossula having parallel sides. It extends almost to the axial end of the cardinal fossula. The counter septum extends to the axis and is slightly elevated and longer than the neighboring major septa. The alar septa are distinctly elevated and extend from points on the calyx margins midway between the cardinal and counter septa to the subcentral axis. This orientation causes them to be directed obliquely toward the axial end of the counter septum. The septa in the cardinal quadrants are longer than those in the counter ones and are directed pinnately toward the cardinal fossula at angles of about 30 degrees. The septa in the counter quadrants are parallel to the counter septum and directed obliquely toward the alar septa at angles of about 30 degrees. The septa in each cardinal quadrant range in number from 28 in smaller coralla to 38 in larger ones. In the counter quadrants they range from 24 to 30. All major septa extend from the periphery to the axis and become twisted and elevated at their axial ends, where they form a small, irregularly shaped axial boss. The minor septa are lower than the major ones and terminate at a point about halfway to the axis. The peripheral parts of the septa are provided with very short, closely set carinae, which appear as small striae along the sides of the septa almost at right angles to their distal surfaces. The carinae terminate above the intercarinate areas, which gives the distal surface of each septum a denticulate appearance. Dissepiments are present only between the peripheral parts of the larger coralla.

In a transverse section of a mature corallum cut just above the proximal point the septa reach the axis and are so dilated that they are in contact throughout their length. In another transverse section cut just below the base of the calyx of the same specimen the septa in the counter quadrants have become attenuate, and a few dissepiments can be seen between their peripheral parts. Carinae are visible as small rounded protuberances along the sides of the septa. In the

cardinal quadrants the septa are still dilated and in contact. Neither dissepiments nor carinae are present.

In a longitudinal section of another corallum the tabulae appear as thin, distally arched tabellae. They are obscured proximally by the stereoplasm of the dilated septa and are best developed just beneath the base of the calyx. On the counter side of the corallum the dissepiments appear at a point about halfway between the proximal point and the margin of the calyx. On the cardinal side they first appear at the base of the calyx wall. All the dissepiments are large and steeply inclined.

Occurrence.—Middle Devonian, Tioghnioga stage, Beechwood limestone; southern Indiana and northern Kentucky, coral bed of Hungry Hollow formation; Thedford, Ontario.

Types.—Hypotypes Nos. 5201, 24823, 24824, 24825, 24826, 24827, 24828, Museum of Paleontology, University of Michigan.

Odontophyllum patellatum (Holmes)

(Pl. 2, Figs. 1-3)

Heliophyllum patellatum Holmes, 1887, pp. 14, 18, 31, pl. 12, figs. 23-25.

Description.—The holotype is a curved patelloid corallum almost 50 mm. in length along the convex side and about 20 mm. along the concave side. The calyx is 53 mm, in diameter along the countercardinal axis and 51 mm. at right angles to it. The epitheca is thick and very coarsely annulated, with the major annulations separated by an average distance of 6 mm. on the convex side of the corallum. The annulations converge toward the concave side, where they are separated by distances of less than 2 mm. On the epitheca are prominent irregularly developed pseudocostae. These are not in a continuous vertical series, but are offset after each major annulation. The calyx has a prominent peripheral platform and a wide, shallow axial pit. The former ranges from 8 to 11 mm. in diameter and is horizontal in the cardinal quadrants and everted in the counter. The latter is subquadrate in outline, averaging about 40 mm. in diameter, with walls sloping gently in the cardinal quadrants and steeply in the counter quadrants toward the axis. The cardinal septum lies in a long, very narrow fossula, and the septa in the cardinal quadrants are directed pinnately toward it as in *O. convergens*. There are thirty septa in each cardinal quadrant. The alar septa are slightly elevated, and the septa of the counter quadrants are directed obliquely toward them. The counter septum is slightly longer than the metasepta. There are twenty-six septa in each counter quadrant. All major septa reach or closely approach the axis and become twisted and elevated at their axial ends, where they form an irregularly shaped boss. The minor septa are unusually long, their axial ends almost reaching the margin of the axial boss. All septa are carinate, but the carinae are very short and appear as fine striae on the sides of the septa. Dissepiments are closely set between the septa in the region of the peripheral platform and are more widely spaced from the inner edge of the platform to a point about halfway down the calyx wall.

Remarks.—The species is easily distinguished from O. convergens, its nearest relative, by its larger size, the division of the calyx into a peripheral platform and a subquadrate axial pit, the greater number of septa, the relatively longer minor septa, the wider dissepimentarium, and the pseudocostate epitheca.

The specimen was originally studied by Carl Rominger, who labeled it *Cyathophyllum patella*, apparently intending to describe it at a later date. Holmes (1887, pp. 14, 18, 31, pl. 12, fig. 23) was the first to describe the species, although on page 14 of her paper she credits Rominger as its author. She changed the trivial name to *patellatum*, and in the fossil list on the same page the species is recorded as "Heliophyllum patellatum Rom."

Occurrence.—Middle Devonian, Tioghnioga stage, Beechwood limestone; Charlestown Landing, Clark County, Indiana.

Type.—Holotype No. 5203, Museum of Paleontology, University of Michigan.

Odontophyllum tornatum (Davis)

(Pl. 2, Figs. 4-6)

Cyathophyllum tornatum Davis, 1887 partim, pl. 86, figs. 7-9, non figs. 10-11, nec pl. 80, fig. 1, which is Odontophyllum convergens (Hall).

Description.—Simple, massive, subpatelloid to trochoid coralla with a rounded, curved conical form. In the majority of specimens

the curvature is sufficient to place the apex directly beneath the margin of the concave side of the calyx. The holotype measures 60 mm. in length along the convex side and about 30 mm. along the concave side. The proximal point is distinctly flattened. The corallum is provided with an epitheca which is finely to coarsely annulated and through which the peripheral edges of the septa are faintly visible. The calvx is round and measures 45 mm, in diameter. The walls slope inward at a moderate angle from the margin to the axis, and no distinct peripheral platform is present. The cardinal septum lies in a deep, wide fossula, and the septa in the cardinal quadrants converge toward it in the typical pinnate manner. The alar septa are not distinctly elevated, but their position can be determined by the abutting of the septa of the counter quadrants against them, which creates faint pseudofossulae. The septa number about thirty in each cardinal quadrant and about twenty-six in each counter quadrant. All major septa reach the axis where they become slightly twisted and elevated. The minor septa average two thirds the length of the major. They usually terminate just before reaching the base of the calvx. All septa are faintly carinate, and the carinae appear as faint vertical striae on the sides of the septa exactly as in O. convergens and O. patellatum. Numerous dissepiments are present between the peripheral parts of the septa. The zone of dissepiments extends inwards about 10 mm, from the calyx margin.

Remarks.—This species can easily be distinguished from either O. convergens or O. patellatum by its taller, more massive, almost trochoid form, by its characteristically flattened proximal point, and by having the axis more centrally located, with the cardinal and counter quadrants of approximately equal size.

Occurrence.—Middle Devonian, Tioghnioga stage, Beechwood limestone; southern Indiana and northern Kentucky.

Type.—Hypotype No. 5202, Museum of Paleontology, University of Michigan.

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EXPLANATION OF PLATE I

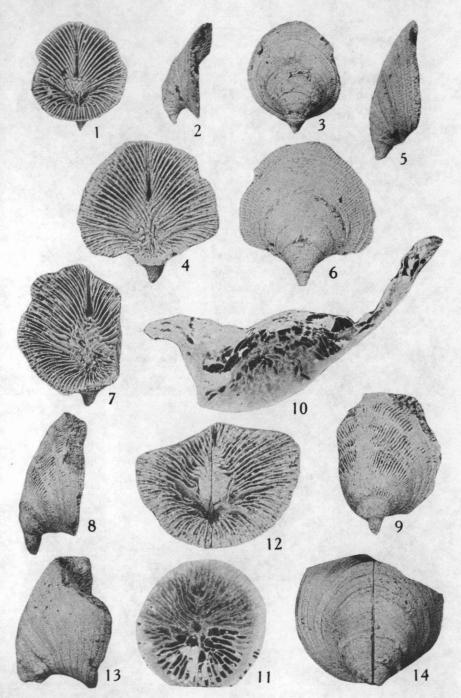
(Figs. 1–9, 12–14 \times 1; Figs. 10–11 \times	×	2	2)
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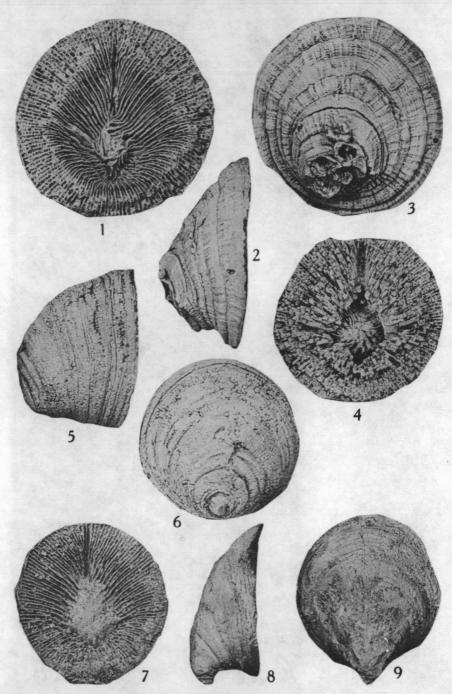
Odontophyl	lum conve	ergens (Hall)			• • • • • •	• • • • •	54
1. Di	stal view	of an	immature	specimen,	showing	the ca	rdinal	and
	counter qu	adrants	, the cardir	al fossula a	and alar p	oseudofo	ossulae,	and
	the dentice	ılate sej	ota. Hypot	ype No. 24	4824. Bee	chwood	limesto	one
	Charlestow	n Land	ing. Clarke	County, Ir	ndiana			

- Side view of the same specimen, showing pronounced curvature of corallum and gentle slope of calyx wall
- 3. Proximal view of the same specimen, showing apical point and convergence of the septa along the cardinal line
- Distal view of a larger specimen with an incomplete calyx. The elevated alar septa are well shown. Hypotype No. 24825. Same horizon and locality as original of Figure 1
- 5. Side view of the same specimen, showing growth annulations
- 6. Proximal view of the same specimen
- Distal view of an incomplete specimen in which the septa are unusually well preserved. The carinae and axial boss also are well shown. Hypotype No. 24823. Same horizon and locality as original of Figure 1
- 8. Side view of the same specimen, showing extreme prolongation of the apical point
- Proximal view of the same specimen. The removal of the epitheca has made the carinae visible on the peripheral edges of the septa
- Longitudinal section of a specimen showing the domed tabellae and the peripheral dissepiments. Hypotype No. 24826. Coral bed of Hungry Hollow formation; Thedford, Ontario
- 11. Transverse section of another specimen cut just below the base of the calyx. This illustrates the late neanic stage with the attenuate septa in the counter quadrants and the dilated septa in the cardinal quadrants. Hypotype No. 24828
- 12. Distal view of a mature specimen in which the incipient peripheral platform along the counter quadrants is well shown. Hypotype No. 24827. Same horizon and locality as original of Figure 1
- 13. Side view of the same specimen, showing slope of calyx margin. The cardinal margin and proximal point are missing "
- 14. Proximal view of the same specimen, showing the well-preserved epitheca with its closely set annulations of growth

STUMM PLATE I



STUMM PLATE II



EXPLANATION OF PLATE II

(All figures \times 1)

	(
Odonto	phyllum patellatum (Holmes)
1.	Distal view of a specimen showing the peripheral platform, quadrate axial pit, quadrantal arrangement of septa, cardinal fossula, and alar pseudofossulae. Holotype No. 5203. Beechwood limestone; Charlestown Landing, Clark County, Indiana
2.	Side view of the same specimen, showing curvature of corallum and convergence of growth annulations toward the concave side
3.	Proximal view of the same specimen, showing the well-developed epitheca and the pseudocostae
Odonto	phyllum tornatum (Davis)
4.	Distal view of a specimen showing the wide cardinal fossula and the centrally located axis. Hypotype No. 5202. From same horizon and locality as original of Figures 1-3
5.	Side view of the same specimen, showing the massive corallum and the flattened apical point.
6.	Proximal view of the same specimen, showing the thin, coarsely annulated epitheca, and the flattened apical point.
Odonto	phyllum convergens (Hall)54
7.	Distal view of a well-preserved specimen, showing the narrow fossula, the alar pseudofossulae, and the carinate septa. Hypotype No. 5201. Coral bed of Hungry Hollow formation; Thedford, Ontario
8.	Side view of the same specimen, showing lateral extent of apical point and the closely annulated epitheca
9.	Proximal view of the same specimen