# HELIOPHYLLUM HALL AND CHARISPHYLLUM N. GEN. (DEVONIAN RUGOSE CORALS) OF THE CANTABRIAN MOUNTAINS (NW SPAIN)

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En el presente trabajo se describen ejemplares pertenecientes a dos especies del género *Heliophyllum (H. chengi* n. sp. y H. sp. cf. H. *halli* Edwards and Haine) y una tercera con ciertos caracteres próximos a los de *Heliophyllum (Charisphyllum altevogti* n. gen., n. sp., Familia? Charysphyllidae), todos ellos procedentes del Devónico Medio de la costa asturiana (NO de España).

Heliophyllum parece haber estado circunscrito durante el Emsiense a la provincia de América del Este, sin embargo, durante el Devónico Medio, pasó a tener una amplia distribución. El género podría haber comprendido dos grupos morfológicos caracterizados por septos delgados y dilatados respectivamente.

Palabras clave: Rugosa, Heliophyllum Hall, Charisphyllum n. gen., Givetiense, Devónico Medio, Zona Cantábrica, España.

[Traducido por la revista]

Specimens of two species of *Heliophyllum* (*H. chengi* n. sp. and *H.* sp. cf. *H. halli* E. and H.) and a third species (*Charisphyllum altevogti* n. gen., n. sp., Family? Charactophyllidae) with some heliophylloid characters are described from Middle Devonian strata on the NW coast of Asturia, Spain (Cantabrian coast, near Gijón).

Heliophyllum seems to have been restricted to the Eastern American Realm during the Emsian but became widespread during Middle Devonian time. The genus may have included two morphologic groups characterized by attenuate and dilated septa respectively.

Keywords: Rugosa, Heliophyllum Hall, Charisphyllum n. gen., Givetian, Middle Devonian, Cantabrian Mountains, Spain.

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Specimens of *Heliophyllum* Hall are abundant in many Lower and Middle Devonian rocks of the Eastern Americas Realm (EAR; northern South America and eastern North America), Appohimchi Province (Oliver, 1977, fig. 11), where they range from the Emsian through most of the Givetian. The genus is so pervasive that the Middle Devonian coral fauna in Eastern North America (ENA) is referred to as the *Heliophyllum* fauna (Hill, 1957, p. P49; Oliver and Sorauf, 1983). The genus is virtually absent from western North America (part of Old World Realm) but occurs in northwestern Africa, Europe, the

southern Urals (?), and Asia (table 1). In these areas specimens are Middle Devonian (mostly Givetian) in age.

The ocurrence and distribution of *Heliophyllum* is of particular interest because it is one of the few EAR endemic coral genera to «escape» from ENA, and the only one to have achieved such a remarkably widespread distribution. The biogeography of Devonian rugose corals and the history and peculiarities of the EAR coral fauna, have been described by Oliver (1973, 1975, 1976a, 1977). The key part played by North Africa and Spain was emphasized in these papers (e.g., 1975, p. 156-158)

and by others. Oekentorp (1975, p. 73-81), in a study of favositid (tabulate) corals from northern Spain, referred to a «North Spanish (Asturian) mixed fauna» because of the presence of ENA, Eurasian, and endemic forms, and Oliver and Pedder (1984) recognized North Africa-Spain as a distinct Old World Realm province.

# HELIOPHYLLUM IN NORTH AFRICA AND SPAIN

Specimens of Heliophyllum, remarkably similar to H. halli from New York, were described from Morocco by LeMaitre (1947). Additional North African «Heliophyllum» have been described and illustrated by Cottreau (1940), Termier and Termier (1950) and Semenoff-Tian-Chansky (1961). Although none of these is as well illustrated as LeMaitre's material, we have no reason to question the identifications. The Heliophyllum of LeMaitre is Givetian (Hollard, 1962); the other North African occurrences are Eifelian and/or Givetian. We have examined additional specimens from Le Maitre's Morocco locality and from Eifelian(?) and Givetian localities in the Western Sahara (in collections of the U.S. National Museum of Natural History; USNM) and find most of them to be close to, or conspecific with, H. halli from New York. In contrast, the single specimen illustrated by Semenoff (1961, p. 293-4, pl. 1, fig. 1; Givetian, Algeria) has thickened septa and is closer to Heliophyllum chengi, here described from Spain.

Spanish *Heliophyllum* specimens were described and illustrated by Altevogt (1968; discussed below). In addition, Joseph and Tsien (1975) illustrated a specimen from the French Pyrenees. Both of these ocurrences are Givetian.

G. Altevogt (1963) and Y. M. Cheng (1969) completed dissertations (Westfälische Wilhelms-Universität Münster) on rugose corals of the Devonian of the Cantabrian coast. Both described and illustrated *Heliophyllum*, and Altevogt (1968, p. 764-6, pl. 2, figs. 5a-c) later published illustrations and a brief description. Specimens from these two collections are the principal basis for this study.

Most of the Cheng and Altevogt dissertation specimens are here described as *Heliophyllum chengi* n. sp. and *H.* sp. cf. *H. halli* E. and H. A few additional specimens are placed in a new charactophyllid (?) genus that re-

sembles both *Charactophyllum* (in septal microstructure) and *Heliophyllum* (in its dissepimentarium and possession of carinae). This is described in the section following *Heliophyllum*. We treat it here because its similarities to *Heliophyllum* and *Charactophyllum* may otherwise cause confusion.

#### **BIOGEOGRAPHIC SUMMARY**

Heliophyllum seems to have been restricted to the EAR during the Emsian. During the Eifelian it appeared in North Africa and western Europe (Germany) and spread as far as Armenia (?) and south China. In the Givetian it was common in North Africa, and is known from additional areas in Europe and Asia (Table I). At this time, it also appeared in western North America where it was rare. The distribution history has been discussed by Oliver (1975, p. 156-158; 1976a, p. 372; 1977, p. 124-9).

Two morphologic groups of *Heliophyllum* are tentatively distinguished. The *H. halli* species group (attenuate septa) is the more common form in Venezuela, ENA and North Africa and occurs in Spain, England, Germany, Poland, Armenia (?), the Gorny Altay (?), Afganistan, China, and western North America. *H. chengi* n. sp., with dilated septa, may represent a second species group. The *«H. chengi* group» may also be widespread, but no definate identification can be made from published illustrations. Possible *H. chengi* group forms were noted from Algeria; additional forms are listed in Table I from England, the Southern Urals and north China.

#### LOCALITIES

All studied specimens are from coastal exposures of the Lower Candás Limestone (as defined by Radig, 1962) SE of Candás Asturias, Spain; Candás is 11 km NW of Gijón on the Cabo de Peñas. The localities are shown by Radig, 1962 (text-plate 10) and by Oekentorp, 1975 (figure 2).

Perán is 0.7 km SE of Candás. Locality Punta de Perán is stratigraphically lower than locality Ría de Perán; in the lower and middle parts of the Lower Candás Limestone.

Pico de Castiello is 1.25 km SE of Candás. The collection locality is in the upper part of the Lower Candás Limestone.

Table I.-Old World Realm occurrences of Heliophyllum as documented by specimens we have been able to examine or by published photographs. For northwest Africa and Spain, see text discussion. 1, ex gr. H. halli; 2, ex gr. H. chengi. All queries (?) are ours and (depending on placement) indicate that we question the presence of Heliophyllum in the geographic area, the identification of genus or species, and/or the species group to which it might be assigned. Additional reported occurrences of Heliophyllum are either inadequately documented, based on misidentifications, or duplicate other, listed forms.

#### Eifelian occurrences:

West Germany; H. dahlemense (Haller), only 3 specimens known; 1.

Armenia (?); H? longiseptatum Sytova; 1.

China, Guangxi Prov.; H. beiliuense Yu and Kuang; 1.

#### Givetian occurrences:

England, S. Devon (?); H? shinneri Middleton; 2.

Somerset; specimens in Webby colln., Bristol; 1.

Poland, Holy Cross Mts.; specimens in USNM (gift of M. Różkowska); 1.

USSR, So. Urals (?); H? aiense Soshkina, 1949 (holotype, pl. 36, figs. 1a-d); 2.

Armenia; H. halli? Soshkina; 1.

Gorny Altai; H. altaica Ivania; 1?

Afghanistan; H. halli? Brice; 1.

China, Qinghai (?); H? qinlingense Cao, 2.

W. North America, Dist. of Mackenzie; H. borealis McLaren; 1.

Great Basin; specimen in USNM; 1.

### SYSTEMATIC PALAEONTOLOGY

# Family ZAPHRENTIDAE Milne-Edwards and Haime, 1850

Genus Heliophyllum Hall, 1846

1846 Cyathophyllum (Heliophyllum) Hall, p. 183. 1976 Heliophyllum Hall. Oliver, p. 123-124; see

for discussion and additional references. 1976 Heliophyllum. Sorauf and Oliver, p. 331-

343; detailed study of carinae and trabecular structure.

1981 Heliophyllum Hall, Hill, p. F296-297; modern diagnosis.

Type species.-Heliophyllum halli Milne-Edwards and Haime (see Lang, Smith and Thomas, 1940, p. 66, for details). Givetian, Hamilton Group, New York.

Diagnosis.—«Solitary and colonial rugose corals, widely varying in shape and type of colony, characteristically having a moderately deep calice with broad axial pit, a steeply inclined lower calice wall, a broad horizontal or gently inclined peripheral platform, and a shallow fossula.

«Major septa tend to be long and are bilaterally arranged about the cardinal-counter plane; mature septa may be attenuate, but septa are moderately to heavily dilated at least in early ontogenetic stages. Carinae are abundant and prominent, commonly long yardarm but short zigzag carinae may also occur; they are commonly, but not necessarily, limited to the dissepimentarium.

«Dissepiments are globose and in numerous rows. Tabulae are incomplete, commonly convex but forming a generally concave pattern.» (Oliver, 1976b, p. 123).

Remarks.-Sorauf and Oliver (1976) described the microstructure of the septa and carinae of New York Heliophyllum. Septa are divided into carinae and intercarinae. Each carina is a single trabecula, or a succession of trabecular clusters along a common axis that may branch. Intercarinal structure is «palisaded», wherein fine, subparallel elements form parts of septa between carinae. The existance of these distinct parts of septa between carinae may be characteristic of the genus and serve to separate Spanish Heliophyllum spp. from associated forms that lack intercarinae.

> Heliophyllum chengi n. sp. Figs. 1 and 2

1968 Heliophyllum halli Edwards and Haime. Altevogt, p. 764-6, pl. 2, figs. 5a-c; not Edwards and Haime, 1850.

Diagnosis.—Small to medium sized Heliophyllum with septa somewhat thickened in the

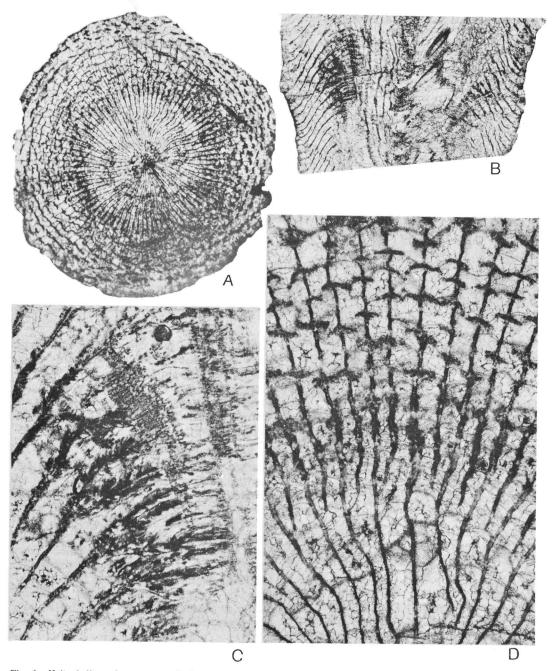


Fig. 1.—Heliophyllum chemgi n. sp. Holotype, Münster B2.45. Transverse and longitudinal thin sections. A-B, x2; C-D, details of same, x10.

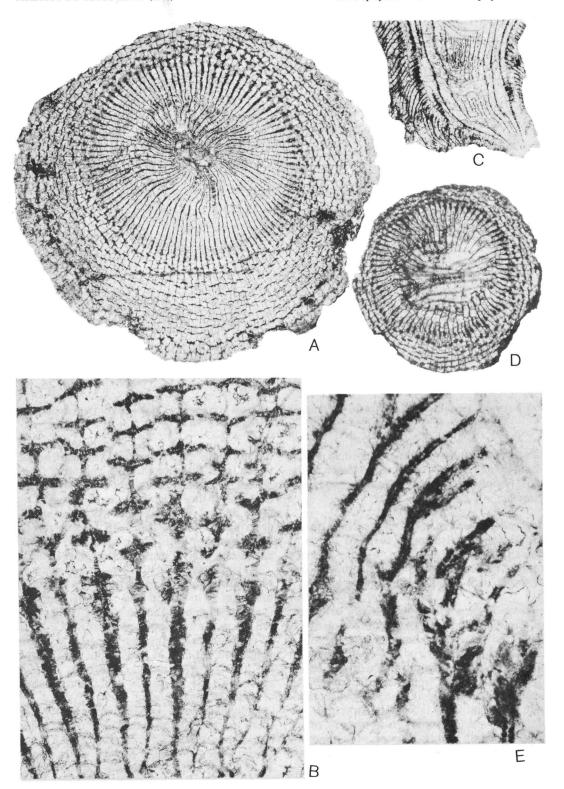
Fig. 2.-Heliophyllum chengi n. sp. Paratypes.

A-B.-Transverse thin section of Münster B2.46, x2, and detail x10.

C-E.-Thin sections of Münster B2.39.

C-D: Longitudinal and tranverse, x2.

E: Detail of C, x25.



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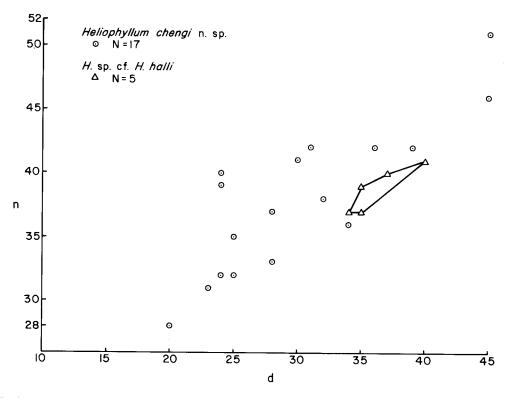


Fig. 3.—Graph of number of major septa (n) versus diameter (d) in mm in samples of 17 Heliophyllum chengi n. sp. and 5 H. sp. cf. H. halli E. and H. The holotype of H. chengi is at n=42, d=36.

tabularium, and with yardarm carinae. Major septa extend from .7 to 1.0 the distance to the axis; peripherally discontinuous in larger specimens.

External features.—Solitary, trochoid to ceratoid horn corals; length to 10 to 12 cm or more; diameters to 4.5 cm. Calices approximately half as deep as their diameter; one example with a calicinal offset is known.

Internal features.—Septa radially arranged, numerous. The cardinal-counter plane is commonly marked by a narrow fossula with a short cardinal septum, or by a counter septum flanked by long counter-lateral minor septa, or by both. Major septa extend from .7 to nearly 1.0 the distance to the axis but septa rarely meet and there is no axial structure. Minor septa are commonly .6 as long as major septa, but only slightly thinner. Major and minor septa may be peripherally discontinuous in coralla with large diameters.

The septa are characteristically thickened in the inner dissepmentarium and outer tabularium. The thick parts of the septa gently taper toward the axis; peripheral thinning is more abrupt. Outside the thickened zone, septa are uniformly thin with numerous yardarm carinae; both outer septa and carinae are thicker than is common in typical *H. halli*.

Major septa number 28 to 51 in sections through the upper parts of 17 corals with diameters of 20 to 45 mm (Fig. 3). Septal number is apparently consistent in mature parts of coralla; e.g. the holotype specimen (B2.45) has 42 major septa in a high section with a 36 mm diameter; but has 41 septa approximately 2 cm lower at a diameter of 26 mm; another specimen (L21.51) has 37 septa at diameters of both 19 and 28 mm.

In longitudinal sections, numerous rows of small, normal dissepiments occupy the outer half of the radius. The structure of the tabularium varies; in coralla with short septa (e.g. B2.37), tabulae are more-or-less complete,

closely spaced, and gently concave except marginally; in specimens with long septa, tabulae are incomplete and irregular.

Septal carinae are dominantly yardarm although some irregular forms are present. Each carina is a single trabecula and most are Type I (Sorauf and Oliver, 1976a, p. 336-339) but in most specimens, some trabeculae branch at low angles and are distinctly Type III. In comparison with *H. halli* from New York, the *H. chengi* carinae are intermediate between Types I and III.

Remarks.—H. chengi is notably variable in the length of major septa and in the amount of septal thickening. It differs from associated specimens of H. sp. cf. H. halli, and from typical H. halli, in the characteristic thickening of mid-parts of septa.

Occurrence.—Lower Candás Limestone (Givetian), Ría de Perán, Punta de Perán, and Pico de Castiello, near Candás, NW of Gijón, Spain (Cantabrian Coast).

Material.—17 specimens: Holotype, Münster B2.45 (Fig. 1A-D); paratypes, Münster B2.37, .38, .39 .40, .46, .47, .387, L21.51, .52 (all from Ría de Perán); Münster B2.57 (Punta de Peran); and Münster B2.33,.34,.35,.36, and USNM 413587 (Pico de Castiello); USNM 413588 (Punta de Perán) is probably this species. The Münster B2 specimens here listed were collected under the direction of Prof. A. von Schouppé and described in the dissertation of Y. M. Cheng (Münster, 1969); the L specimens were collected by Dr. F. Radig and described by Altevogt (1968); the USNM specimens were collected by Oliver in 1969, under the guidance of K1. Oekentorp and G. Altevogt (Münster).

# Heliophyllum sp. cf. H. halli E. and H. Fig. 4

Diagnosis.—Medium to large Heliophyllum with long, attenuate septa and short yardarm and zigzag carinae.

External features.—Solitary, ceratoid-cylindrical horn corals; length up to 20 cm or more; diameters to 5 cm. Calices not known; configuration of dissepiments and tabulae suggets that they were broad and shallow. One individual (B2.41) has 5 peripheral offsets in the calice.

Internal features.—Septa radially arranged and numerous. In thin sections the cardinalcounter plane is commonly marked by 1 or 2 short major septa. Other major septa extend nearly or quite to the axis rarely meet and no axial structure is formed. Minor septa are commonly .5 to .7 as long as the major septa. The major septa are very irregular, even contorted, within the tabularium.

Mature septa are uniformly attenuate except for their peripheral ends which are wedge-shaped. Carinae are short and tend to be irregular, either yardarm or zigzag, both types appearing in most sections. Major septa number 37 to 40 in the upper parts of 5 corals at diameters of 34 to 40 mm (Fig. 3).

In longitudinal section, dissepments are small to medium size, normal to globose; peripheral rows are composed of the larger, more globose types. The width of the dissepimentarium is more than half the radius. Tabulae are incomplete, where distinguishable they are gently concave and closely spaced.

The carinae, as seen in longitudinal section, are thin. Each is a single monacanthine trabecula that is thickest in the center of the septum. The carinae are Type IA of Sorauf and Oliver (1976, p. 336-339).

Remarks.—H. sp. cf. H. halli differs from associated H. chengi in its very attenuate septa and carinae; it falls within the range of variation that we recognize in H. halli from the Hamilton Group of New York, but larger suites of specimens are needed to fully assess the Candás species and its relationships.

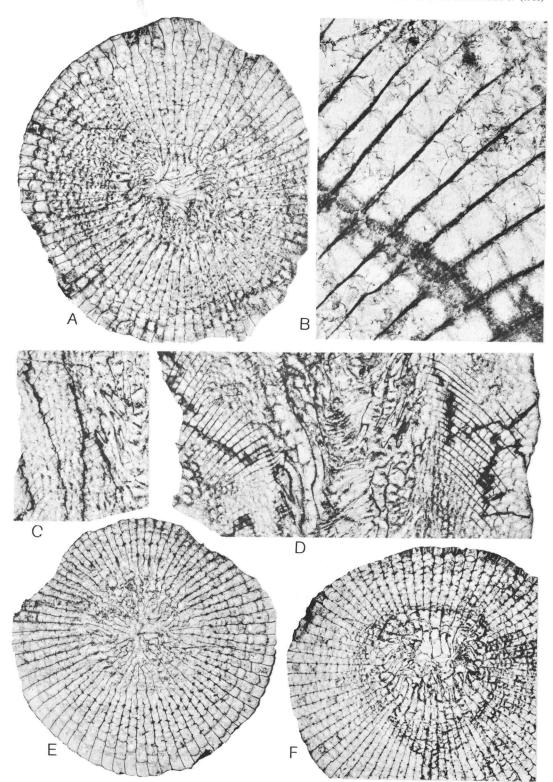
Occurrence.—Lower Candás Limestone (Givetian), Pico de Castiello and Ria de Perán, near Candás, NW of Gijón, Spain (Cantabrian Coast).

Material.—Five specimens: Münster B2.41, .42, .289, and .388 (Pico de Castiello), and B2.386 (Ría de Perán); collected under the direction of Prof. A. von Schouppé.

# Family? CHARACTOPHYLLIDAE Pedder, 1972 Genus *Charisphyllum* n. gen.

Type species.—Charisphyllum altevogti n. sp. Lower Candás Limestone (Givetian) near Candás, NW of Gijón, Spain (Cantabrian Coast).

Diagnosis.—Solitary rugose corals possessing yardarm carinae formed by charactophylloid trabeculae that are commonly at a high angle in the dissepimentarium. Major septa long; in transverse section shaped like an



elongate spear with carinate shaft, and head tapering to a fine, attenuate point. Wide dissepimentarium includes numerous rows of globose, equal-sized dissepiments that may be obscured by the carinae/trabeculae in longitudinal sections. Minor septa well developed, markedly thinner than majors. Septa radially arranged, commonly with no apparent modification of the protosepta.

Remarks.—Charactophylloid trabeculae (Pedder, 1972, p. 698) are thick monocanths that incline outward near the corallite wall, bend toward the axis within the outer dissepimentarium (becoming horizontal or inwardly inclined in some forms), then bend sharply upwards at the margin of the tabularium. The charactophylloid flexure is well shown in Charisphyllum (Figs. 6C, D, 7E, G) but the inclination within the dissepimentarium varies from gently to steeply outward (compare figures 5D and 7E). The trabeculae are thick, feathery monocanths like those of Charactophyllum but the trabeculae are at a higher angle, and the flexure is less pronounced than in that genus. Trabecular growth in the charactophyllids was apparently uniform, producing evenly spaced fibers at a constant angle to the trabecular axis. This is in contrast to trabecular growth in *Heliophyllum* wich seems to have been episodic, producing monocanths that are typically a succession of tufts (see Sorauf and Oliver, 1976).

Charisphyllum differs from Charactophy*llum* in the orientation of the trabeculae (discussed above), in lacking rhopaloid major septa, and in having incomplete rather than commonly complete taabulae. It is similar to Piceaphyllum Rózkowska (1979) in some respects but differs in having well developed minor septa and very simple major septa, uncomplicated by peripheral splitting.

Specimens of Charisphyllum with well-developed, steeply inclined carinae are similar to Heliophyllum in some respects. However, they differ in trabecular microstructure and configuration, as discussed above, and in lacking intercarinae and a cardinal fossula.

Distribution.—In addition to the Candás species, Charisphyllum is known to occur in Middle Devonian rocks of the Western Sahara and Moravia(?) and may occur in the Southern Urals (see discussion under C. altevogti).

## Charisphyllum altevogti n. sp. Figs. 5-7

External features.—Small to medium-sized, trochoid horn corals; length to 6 cm or more, diameters to 4 cm. Calices moderately deep with broadly convex sides descending to narrow axial pit. Septa attenuate within calice, with numerous yardarm carinae; no fossula. Calicinal offsets known in one specimen (Fig. 7B).

Internal features.—Septa numerous, radially arranged. Cardinal and counter septa and the C-K plane are commonly not recognizable in sections. Major septa straight, extend approximately .8 the distance to the axis; from this point a few may continue by an irregular course to the axis and meet, but no axial structure is formed. Minor septa are nearly as long as the straight parts of the major septa, but are markedly thinner.

The septa are thickened at the inner margin of the dissepimentarium; thickened yardarm carinae are variably developed across the whole dissepimentarium. Each carina is a single monocanthine trabecula that directly adjoins the next carina/trabecula. In transverse sections the crossbars can be relatively long so that carinae of adjacent septa touch (Fig. 5B), giving the appearance of a grid. In the axial plane of the septa, trabeculae average 0.4 mm in thickness. Major septa number 28 to 37 in sections through the upper parts of 10 corals with (section) diameters of 13 to 38 mm (Fig. 8).

In longitudinal sections, numerous rows of small, normal, globose dissepiments occupy

Fig. 4.-Heliophyllum sp. cf. H. halli E. and H. Thim sections.

A-B, D.-Münster B2.42.

A, D: Transverse and longitudinal, x2.

B: Detail of D, x10.

C, E.-Münster B2.289. Part of longitudinal and transverse, x2.

F.-Münster B2.41. Transverse, x2.

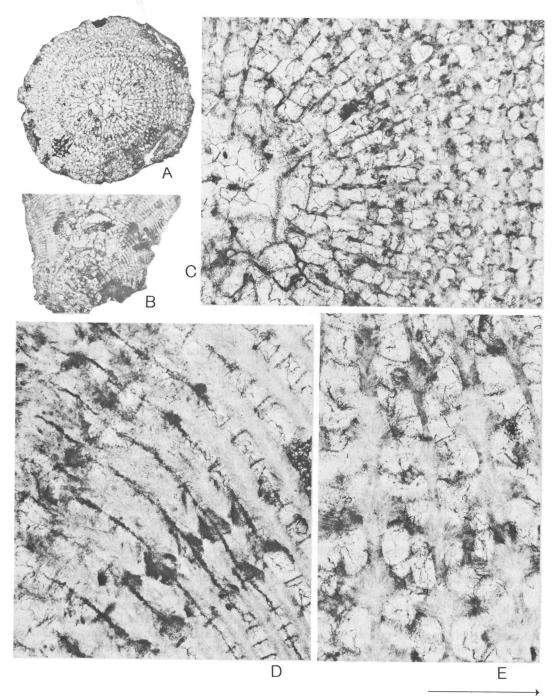


Fig. 5.—Charisphyllum altevogti n. gen., sp. Holotype, Münster B2.28. Transverse and longitudinal thin sections.

A-B: Transverse and longitudinal, x2. C, E: Details of A, x10 and x25.

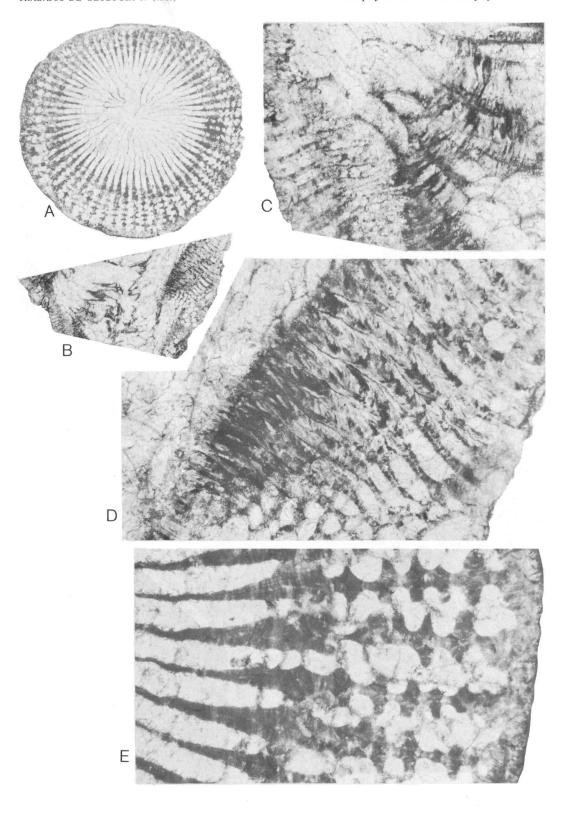
D: Detail of B, x25.

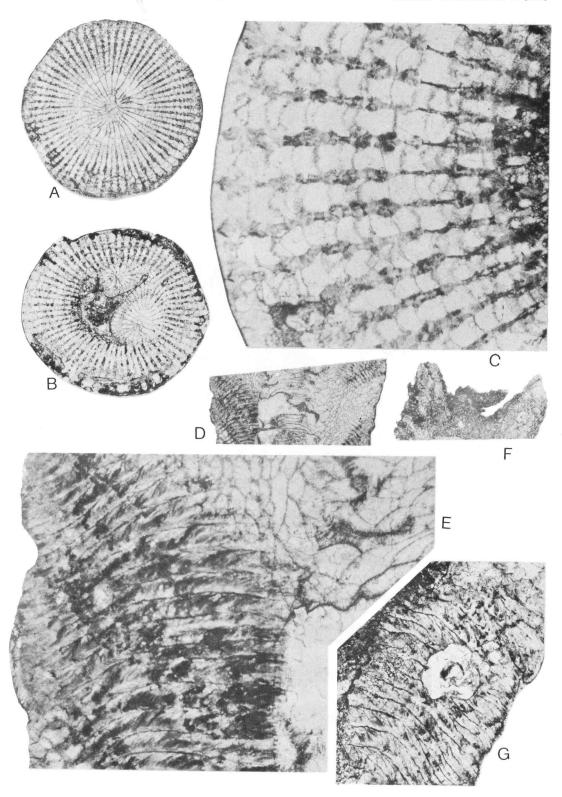
Fig. 6.—Charisphyllum altevogti n. gen., n. sp. Paratype, Münster 2.56.

A-B: Transverse and longitudinal thin sections, x2.

C-D: Details of B, x10.

E: Detail of A, x10.





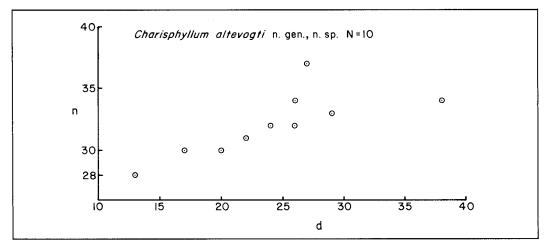


Fig. 8.—Graph of number of major septa (n) versus diameter (d) in mm in Charisphyllum altevogti n. gen., n. sp. Sample of 10 specimens. The holotype is at n = 31, d = 22.

the outer thirds of the corallite. The dissepimentarium is traversed by the carinae/trabeculae that are marginally steep, more gently inclined inward, but bent upward in the tabularium (charactophylloid trabeculae of Pedder, 1972, p. 688). Trabeculae are feathery monocanths. Tabulae are incomplete, short arched plates, commonly tabellae-like; the tabularium occupies the center third of the corallum.

Remarks.—C. altevogti is characterized by having vardarm carinae that are markedly thickened below the calice. In the calice, specimens are similar to associated Heliophyllum but lack the fossula of that genus. In sections, the charactopylloid microstructure is well developed but the inclination of the trabeculae varies widely (Figs. 5-7).

C. altevogti is very similar to an undescribed species from the Western Sahara (Eifelian? or Givetian). Eight specimens of this form (USNM) have been thin sectioned; collectively they show much of the variation seen in C. altevogti and may be conspecific.

Spinophyllum conicum Kettnerova (1932, p. 55-56, 92-93, text-fig. 41) from the Celechovice Limestone (Givetian), Moravia is probably a Charisphyllum. This statement is based on examination of the type specimen in Prague and of a specimen in the USNM fortuitously collected at the type locality by Oliver during August 1986. C. conicum differs from C. altevogti in having relatively short major septa and complete tabulae. Cheng (1969 dissertation) noted the similarity of some of the Candás specimens to Kettnerova's species and referred them to Charactophyllum conicum (Kettnerova) 1932.

One paratype of Heliophyllum aiense Soshkina, 1949 (pl. 36, figs. 2 and 5) may be *Charis*phyllum also; septa have the characteristic spear shape in transverse section and the carinae show the charactophylloid flexure in longitudinal view, but the detailed microstruc-

Fig. 7.—Charisphyllum altevogti n. gen., n. sp. Paratypes.

A-E.-Münster B2.55. Thin sections.

A-B: Lower and higher tranverse sections, x2. Lower section taken below calice; higher section shows two offsets in calice.

C: Detail of B, x10.

D-E: Longitudinal section, x2, and detail of same, x10.

F-G.-Münster B2.391. Longitudinal thin section, x2; and detail of same, x10.

ture of the carinae/trabeculae is not clear. The specimen is reportedly Givetian, and from the Southern Urals.

Occurrence.—Lower Candás Limestone (Givetian), Punta de Perán and Ría de Perán near Candás, NW of Gijón, Spain (Cantabrian Coast).

Material.—11 specimens: Holotype, Münster B2.28 (Fig. 5A-E); paratypes, Münster B2.29, .31, .56, .58, .390, and .391 (Punta de Perán); and Münster B2.51, .54, .55, and .430.1 (Ría de Perán). The specimens were collected under the direction of Prof. A. von Schouppé and described in the dissertation of Y. M. Cheng (Münster, 1969).

#### **ACKNOWLEDGEMENTS**

This study of Givetian Heliophyllum from the north coast of Spain is a part of our continuing restudy of the genus and its species. Dr. Klemens Oekentorp (Münster) loaned us the Heliophyllum and Heliophyllum-like corals from the collections studied by G. Altevogt and Y. M. Cheng (Ph. D. dissertations, Westfälische Wilhelms-Universitäa Münster, 1963, 1969). One of us (Oliver) did preliminary work on the collections, and discussed them with Drs. Altevogt, Cheng and Oekentorp, during an NSF sponsored visit to Münster in 1969. Subsequently, Oliver visited and collected from the Candás localities with Dr. Altevogt and Oekentorp: two specimens of Heliophyllum collected at that time are included in this study. We are indebted to

Dr. Oekentorp, Westfälische Wilhelms-Universitäat Münster, to Dr. Altevogt (Münster), and to Dr. Cheng, now National Taiwan University, for their cooperation and many kindnesses over the years.

All specimens from the Altevogt and Cheng dissertation collections are preserved in the Forschungsstelle für Korallenpaläozoologie, Münster (Münster numbers in specimen lists). The two specimens collected by Oliver are in the U.S. National Museum of Natural History (USNM numbers).

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