Lower Devonian (Emsian) rugose corals from the Cantabrian Mountains, northern Spain

STEFAN SCHRÖDER and FRANCISCO SOTO

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Two species of Lower Devonian rugose corals are described from the Cantabrian Mountains of Spain: *Cantabriastraea cantabrica* gen. et sp. nov. and *Tabulophyllum bonarense* sp. nov. The development of root- or buffer-like attachment structures ("rhizoid processes") in *T. bonarense* indicates adaption to the soft substrate and supports corallite stabilisation. Because of their strongly everted calices and a corresponding arrangement of trabeculae, the colonies of the genus *Cantabriastraea* are assigned tentatively to the Paradisphyllinae, constituting the first record of the subfamily in Western Europe. Some specimens give information on colony-formation of this taxon, which is induced by strong lateral budding (nonparricidal increase) of a remarkable large and long-lasting protocorallite.

Key words: Rugosa, *Cantabriastraea*, *Tabulophyllum*, Devonian, Emsian, Cantabrian Mountains, ecology.

Stefan Schröder [ste.schroeder@gmx.net], Geologisches Institut, Zülpicher Strasse 49A, D-50674 Köln, Germany;
Francisco Soto [fsoto@geol.uniovi.es], Departamento de Geologia, Universidad de Oviedo, c/ Arias de Velasco s/n, E-33005 Oviedo, Spain.

Introduction

During the last 150 years a wide range of Palaeozoic fossils has been described from the Cantabrian Mountains and with regard to Devonian faunas the so-called "Sabero-fossils" are especially famous. Verneuil (1850) was the first to give formal descriptions of numerous Devonian trilobites, blastoids, crinoids, and mainly brachiopod species from the "district of Sabero (Léon)", which became later known as "Sabero fossils". In contradiction to the applied name, this fauna did not derive exactly from Sabero, but from villages close to it, for example Colle, Collado de Llama, Aleje, Alejico, Peña Venera, and other localities (Verneuil 1850; Mallada 1875; Bayle 1878; Bergonioux 1938; Comte 1938, 1959). The village of Sabero itself is situated in a Stephanian basin (Fig. 1).

Many taxa of fossils mentioned from Colle (more than a hundred known species) occur in the Lower Devonian La Vid Group (Fig. 2), composed of 240–250 m of siliciclastic and carbonate rocks. Most of these fossils occur at the top of the La Vid Group, in the Upper Emsian Coladilla Formation, consisting of crinoid limestones, mudstones and shales (Fig. 2). However, some of the "Sabero fossils" derive from other stratigraphical units, both older and younger than the Coladilla Formation, i.e., La Pedrosa and Valporquero Formations (Arbizu 1979; Arbizu et al. 1996; Truyols-Massoni 1981; Alvarez 1999a, b) and Santa Lucia and Portilla Formations (Breimer 1971; Alvarez 1999a; Schröder 2001; Coen-Aubert 2002).

The rugose corals studied in this paper were sampled directly at Colle and have been collected in the beds COL A-1 (Valporquero Formation), COL A-13-B-1 and COL B-3 (Coladilla Formation) (Fig. 2).

Sedimentological investigations by Truyols et al. (1984), Keller (1988) and Vera de la Puente (1989) suggested that the lower part of the La Vid Group (Felmin Formation) corresponds to a supra-tidal environment, while the upper part (La Pedrosa and Coladilla Formations) was deposited in a sub-tidal, more or less winnowed environment. In the more fossiliferous Coladilla Formation, specimens are internally and externally very well preserved (Alvarez 1990, 1999a). Moreover, usually complete and articulated brachiopod shells are not oriented at all. Some morphological adaptations of the brachiopod shells (Alvarez and Taylor 1987; Alvarez 1999a) and the mineralogical signature of the soft matrix (Alvarez and Brime 1982) indicate a quiet depositional environment, close to the shore, with warm and well oxygenated waters.

The strong endemism of the fauna known from Colle, which is manifested among brachiopods (Alvarez 1990; Garcia-Alcalde 1996, 1999), crinoids (Breimer 1962) and trilobites (Arbizu 1979, 1982; Smeenk 1983) has also been recognized in the rugose corals, preventing direct comparison with other contemporaneous faunas. Lower Devonian (Emsian) coral faunas are generally rare in Europe and only a few, rather isolated localities are known (Montagne Noire, Armorica, Carnic Alps). These faunas do not show a uniform composition and accordingly are usually interpreted as belonging to isolated crustal fragments in paleogeographic reconstructions. Emsian paleogeography, especially in regard to southwestern Europe, is far from well understood and the description of the Spanish fauna is another step in understanding the paleogeographic puzzle in this region. The recent discovery of a Emsian *Synaptophyllum* biostrome in the
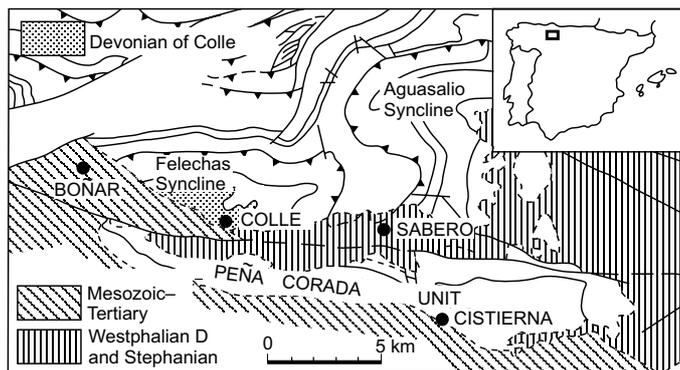
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Fig. 1. Geographical and geological location of Colle (modified from Garcia-Alcalde 1999).

Montagne Noire (Moulin de Garel, SW Cabrieres) is the second known European occurrence aside of Colle and may indicate a connection to the Spanish fauna.

Institutional abbreviation.—The collection described in this paper is deposited in the Departamento de Geologia, Universidad de Oviedo, Oviedo, Spain, abbreviated DPO.

Systematic palaeontology

Subclass Rugosa Milne-Edwards and Haime, 1851
Order Stauriida Verrill, 1865
Family Kyphophyllidae, Wedekind 1927
Subfamily Kyphophyllinae, Wedekind 1927
Genus *Tabulophyllum* Fenton and Fenton, 1924

Type species (by original designation): *Tabulophyllum rectum* Fenton and Fenton, 1924.

Diagnosis.—See Sorauf 1989: 33.

Remarks.—In general, only solitary corals are currently assigned to the genus *Tabulophyllum*, and the classification of colonial forms as *Tabulophyllum* by Soshkina (1952), Bulvanker (1958) and Ivaniya (1965, 1980) has been rejected (McLean and Pedder 1987; Sorauf 1989). The new species of *Tabulophyllum* described herein is apparently solitary but displays a distinctive growth known as "quasi-colonial" and such solitary species with few lateral offsets should also be included in the generic concept of *Tabulophyllum*.

Similar structures are also known from the closely related kyphophyllid genus *Tarphyphyllum* McLean and Pedder, 1984. Its type species *T. besti* McLean and Pedder, 1984 is a solitary species developing few offsets (McLean and Pedder 1984: pl. 11: 4, 7, 10), whereas one paratype is weakly branching to fasciculate (McLean and Pedder 1984: pl. 10: 12). Internally *Tarphyphyllum* differs from *Tabulophyllum* only in having a more strongly developed stereozone of dilated septa, masking the dissepiments, a more simple tabularium, and less numerous dissepiments. Because of the striking resemblances between both genera Sorauf (1998: 49) suggests that *Tarphyphyllum* should rather be regarded
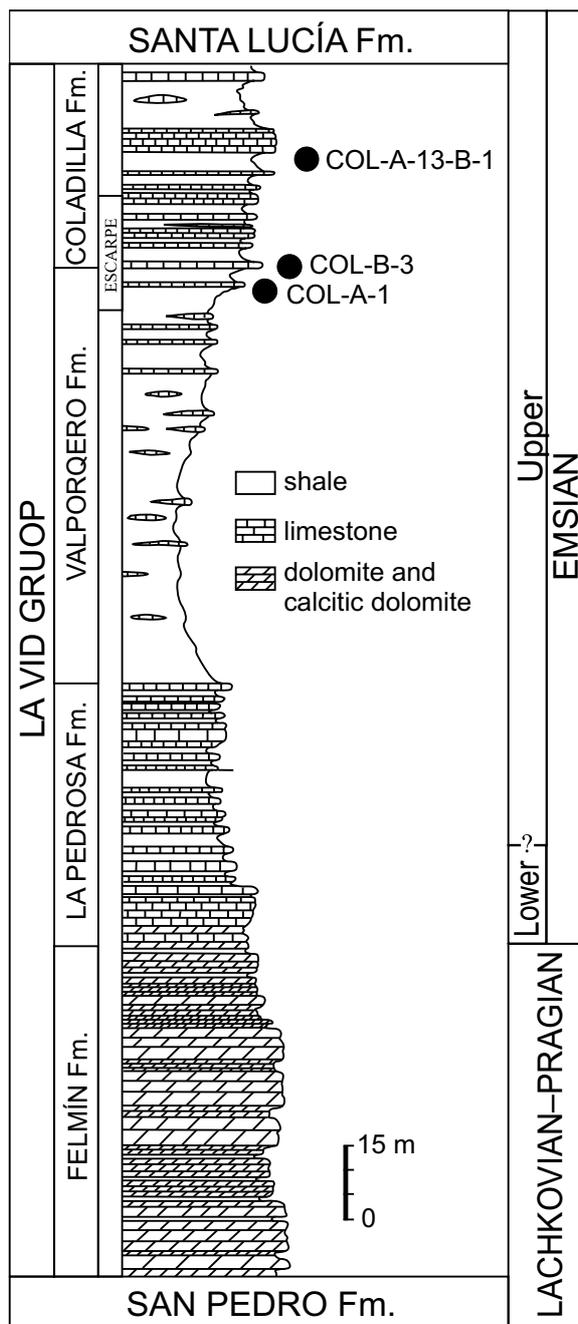

Fig. 2. Stratigraphical section at Colle (Lower Devonian), with location of beds where the studied rugose corals occur (modified from Garcia-Alcalde 1999).

as subgenus of *Tabulophyllum*. Probably some of the weakly colonial species previously assigned to *Tabulophyllum* should be removed to *Tarphyphyllum*. Colonial species of *Tarphyphyllum* may also be very difficult to separate from *Smithiphyllum* Birenheide, 1962 (McLean and Pedder 1984: 28; Sorauf 1998: 49).

Occurrence.—The stratigraphic occurrence of *Tabulophyllum* is mainly Upper Devonian and the genus is globally distributed in the Frasnian. Only a few species are known from the Lower Devonian of Australia and Belgium (Tsien

1977; Hill 1942; Sorauf 1989; Zhen 1995). However, the known Lower Devonian species assigned to *Tabulophyllum* closely resemble the Upper Devonian forms in their general morphology, with long major septa commonly interrupted by large lonsdaleoid dissepiments.

Tabulophyllum bonarense sp. nov.
Figs. 3A–D, 4A–I, 5A–D, 9D, E.

Holotype: DPO 14670 (Fig. 4A, B).

Type locality: Colle, ca. 5 km SE of Boñar, Province León, Hoja 104 (Boñar), 1°33'37''E/42°50'42''N.

Type horizon: Lower Devonian, Emsian, La Vid-Group, brown shales in the lower part of the Coladilla Formation [Col A-13-B-1].

Derivation of the name: After the village Boñar, Province of Leon.

Paratypes: 17 specimens, DPO 14671–14688.

Diagnosis.—Small solitary corals or "quasi-colonies" with a corallite diameter of 12–15 mm and 18–21 short major septa. Septa peripherally commonly interrupted by lonsdaleoid dissepiments. Minor septa are rudimentary and frequently reduced to spines on wall or dissepiments. Narrow dissepimentarium, of 1–2 rows of elongate dissepiments.

Description.—The fragments of corallites are cylindrical, with a maximum length of 5 cm and a diameter of 12–15 mm. Some specimens (Figs. 3B, 5A, D) show preserved offsets developed by lateral increase and some isolated fragments with small diameter (8 mm) should probably be regarded as fragments of such offsets. Preserved calices are shallow funnel shaped (Fig. 3C). Fragments are generally long and cylindrical, and only a few specimens are slightly curved. Rejuvenescence occurs very often and is easily recognized because the expansions of lonsdaleoid dissepiments usually show a sharp boundary (Fig. 3D). Commonly rejuvenescence occurs together with minor shifting of the growth axis. In places structures similar to connecting processes are developed by periodical expansion of lonsdaleoid dissepiments (Figs. 3A, 4I), which usually are only preserved as short spines with thin, irregularly spaced transverse partitions (Fig. 5C). If complete, those structures are blind-ending hollow tubes (Fig. 4I top left, 4C left corallite) and a presumed function as connecting tubulae in contact with possible neighbouring corallites is not definite. In addition to very fine rugae, the wall sometimes shows widely spaced stronger folds, but there is no obvious cyclicity.

Corallite walls are slightly thickened, 0.3–1 mm wide and show a structure of "fibrous crystallites" (Fig. 9D) comparable to the structure of the septotheca observed in *Tabulophyllum* species by Sorauf (1997: 232, fig. 4.2, pl. 1: 7; 1998: 34). If septa are inserted at the wall additional thickenings are possible because of thickened septal bases, but depending on the common development of the lonsdaleoid dissepiments septa are usually interrupted by thin but elongate presepiments which are arranged in up to three rows (Fig. 9E). The innermost row may be of globose shaped dissepiments. In juvenile corallites or offsets septa are usually inserted at the wall and lonsdaleoid dissepiments are not developed in
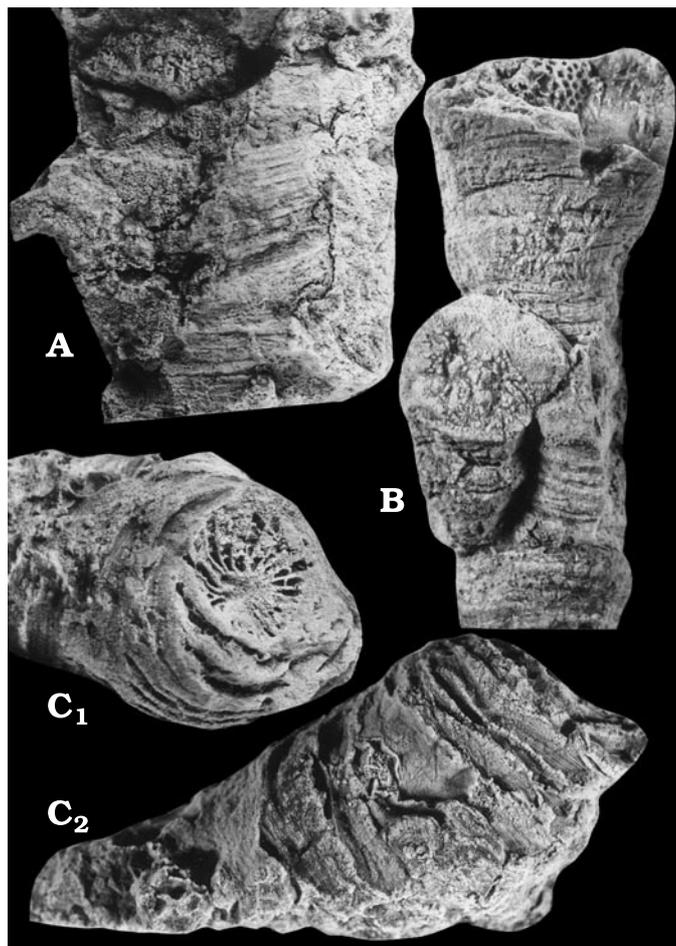

Fig. 3. *Tabulophyllum bonarense* sp. nov., external morphology of corallites. **A**. Corallite DPO 14686 with incomplete lateral projection of connecting process on left side. **B**. Specimen DPO 14678 with two incomplete lateral offsets. **C**. Corallite DPO 14679 with septa interrupted by lonsdaleoid dissepiments in distal view (C_1). Side view (C_2) showing flat base and weak development of talon structures. All × 3. All specimens from the Upper Emsian of Colle.

this stage (Fig. 5D). Major septa range in number from 18–21, but it is impossible to count them correctly in some cross sections in which septa are rudimentary and only recognizeable as short spines extending 1–2 mm into the corallite. Accordingly, there is always a large axial space free of septa, which measures up to 7 mm and is traversed by few, mostly thickened sections of tabulae. Although minor septa are usually developed, they are generally very short and reach up to half of the length of major septa.

Longitudinal sections are simply structured and show a small lonsdaleoid dissepimentarium and a tabularium which is 6–10 mm wide and contains mainly complete tabulae. Tabulae are usually flat, but can be slightly arched. There are 8–10 tabulae/cm corallite-length. Dissepimentarium comprises 1–2, rarely 3 rows of medium sized, elongated, sometimes even sickle-shaped dissepiments. Close to the corallite-wall they are traversed by fine trabeculae, which are weakly inclined.
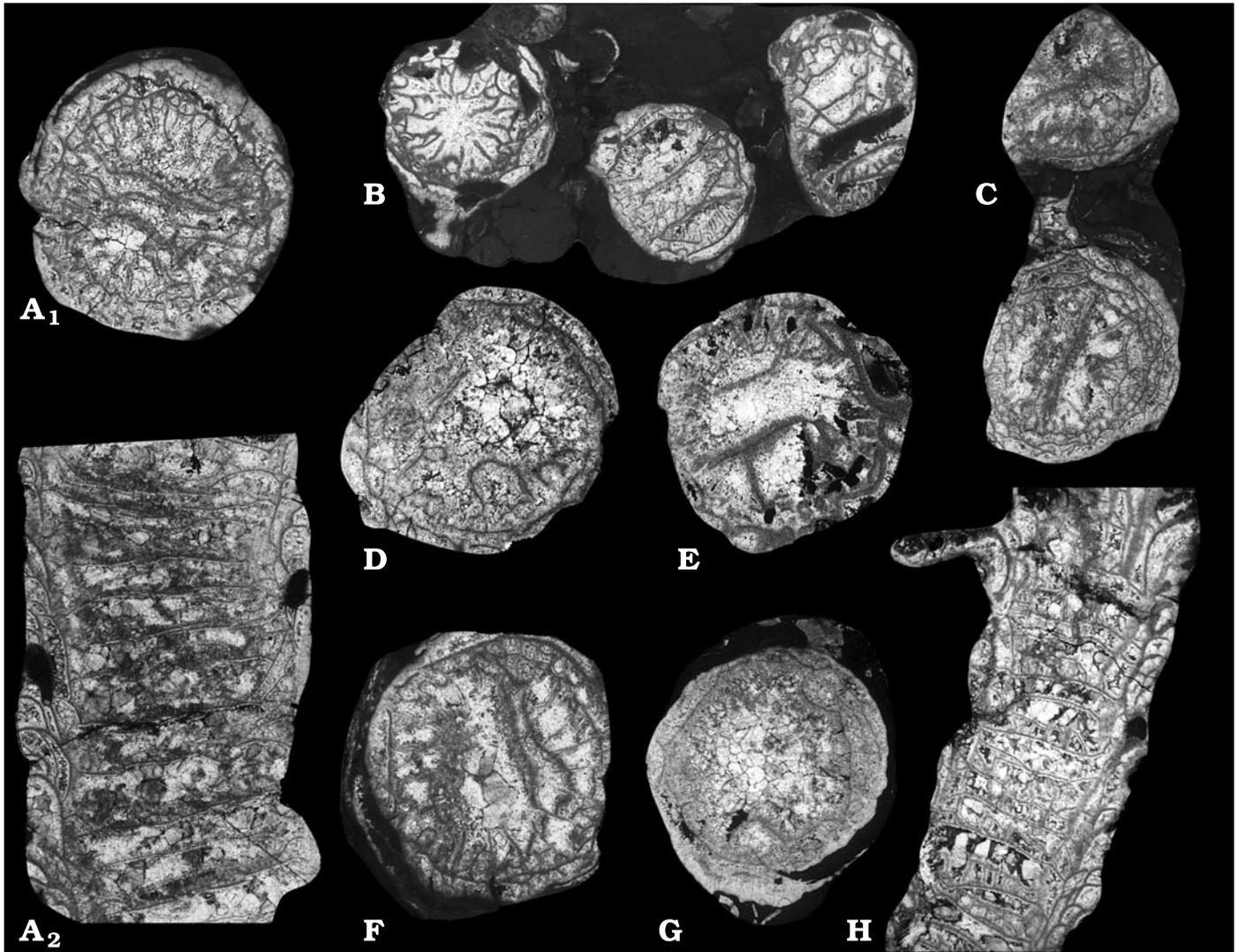
Fig. 4. *Tabulophyllum bonarense* sp. nov. **A**. Holotype DPO 14670 in cross section (A$_1$) and longitudinal section (A$_2$), with narrow dissepimentarium. **B**. Fragment of corallite DPO 14673 with lateral offsets. Well developed major septa are frequently interrupted by lonsdaleoid dissepiments. **C–G**. Cross sections of isolated corallites, showing variable development of septa: DPO 14688 (**C**), DPO 14685 (**D**), DPO 14672 (**E**), DPO 14671 (**F**), DPO 14686 (**G**). **H**. Longitudinal section with a "rhizoid process" on left side of corallite. All × 3, except B, which is × 2. All specimens from the Upper Emsian of Colle.

Remarks.—Although strongly fragmentary, the available material suggests a solitary growth form, with development of rare lateral offsets (Figs. 3B, 4C: above left corallite, 5A, D) which have not reached maturity. This is important, as a specimen should be defined as colonial only in case if its offsets reach morphological maturity (Fedorowski 1978). The existence of underdeveloped offsets, which is not related to extrinsic factors, is most probably genetically controlled and such offsets are known as "lost structures" (Fedorowski 1978). The corresponding corallites are regarded as "quasi-colony" as defined by Fagerstrom and Eisele (1966) or as "simple budding forms" (Minato and Rowett 1967). A comparable morphology has been well documented for *Cratero-phyllum verticillatum* Barbour, 1911 from the Carboniferous of Nebraska and for Permian *Heritschioides* specimens from New Mexico (Fedorowski 1978: pl. 23: 9). However, the best preserved corallite of our material does not show lateral

budding in verticils consisting of numerous offsets arising at the same time as in *C. verticillatum* (Fagerstrom and Eisele 1966: pl. 73: 1, 4), but a more irregular, randomly arrangement (Fig. 3B).

T. bonarense is a morphologically very simple form and differs strongly from its rather large and septal-rich Upper Devonian relatives. Accordingly, there are only a few species of *Tabulophyllum* which may be compared to *T. bonarense* sp. nov., but generally occur in much younger strata. A closely related species seems to be *Tabulophyllum mani-festum* Spasskiy, 1971 (in Dubatolov and Spasskiy 1971) from the Eifelian of the Altai Mountains. This species has also short major septa which are interrupted by lonsdaleoid dissepiments, whereas minor septa are strongly reduced (Spasskiy 1960: pl. 1: 3, 4, pl. 2: 1–6, pl. 3: 1, 2). It is distinguished from *T. bonarense* in having a larger corallite diameter, a much higher number of septa and its strong calicinal

budding, indicating an incipient coloniality as defined by Fedorowski (1970: 603). *Cyathophyllum timanicum* Lebedew, 1902 (Frasnian?, Uchta River, Timan) has a higher number of longer, more regularly developed major septa (26–29 SI) and a stronger development of the lonsdaleoid dissepimentarium (Lebedew 1902: 134, 179, pl. 5: 64–66). However, the classification of some morphologically insufficiently known corals assigned to *Tabulophyllum* remains questionable. This is the case with *Tabulophyllum angulosum* Spasskiy, 1971 (in Dubatolov and Spasskiy 1971: 106, pl. 38: 1), which has been described form the Givetian of the Dzhungarian Alatau or *Calophyllum tchernyschewi* Lebedew, 1902, which is known from the Frasnian of the Timan. Detailed information is lacking on growth form of those species and they are difficult to assign with certainty to *Tabulophyllum* and may belong to *Smithiphyllum*.

Growth form variation in *Tabulophyllum bonarense*

The specimens of *Tabulophyllum* described above show some interesting features concerning growth form which should be discussed in regard to the ecological conditions under which they lived. Some corallites show minor rejuvenescences, which are generally accepted as reaction of the polyp to high environmental stress caused by unfavourable ecological conditions (Scrutton 1998: 16), leading to size reduction of the polyp. Aside from more regular rejuvenescences, which probably were induced by seasonal cyclicity, any other possible factors responsible for such rejuvenescenses are highly speculative (e.g., breeding periods), but in this case constant accumulation of fine-grained sediment (silty marls) may be responsible for triggering this reaction.

The occurrence of these corals is limited to a single stratigraphic level, characterized by the development of numerous small scale mud-mounds, which are intercalated within thin-bedded crinoid limestones. The mounds consist mainly of green polymicritic mud- to floatstones and are rich in bryozoans and crinoids (Schmid et al. 2001: 363, figs. 22, 23). Specimens have been sampled in the intermound facies, which is characterized by sedimentation of very fine marls and limestones. They were living most probably close to the mounds under conditions of low water energy in a quiet environment, which was only slightly illuminated, because of the bathymetric position and continuous sedimentation. Aside from nutrition-factors, those aspects most probably limited corallite growth or were responsible for any growth form modifications, but unfortunately the material is too fragmentary to allow a detailed taphonomic discussion.

Many specimens show weak "rhizoid processes" (Scrutton 1998: 5, fig. 4g), developed by the extension of lonsdaleoid dissepiments (Figs. 3A, 4C, F, I, 5B, C) and sometimes they also possess root- or talon-like structures. Such modifications are obviously ecologically induced and were
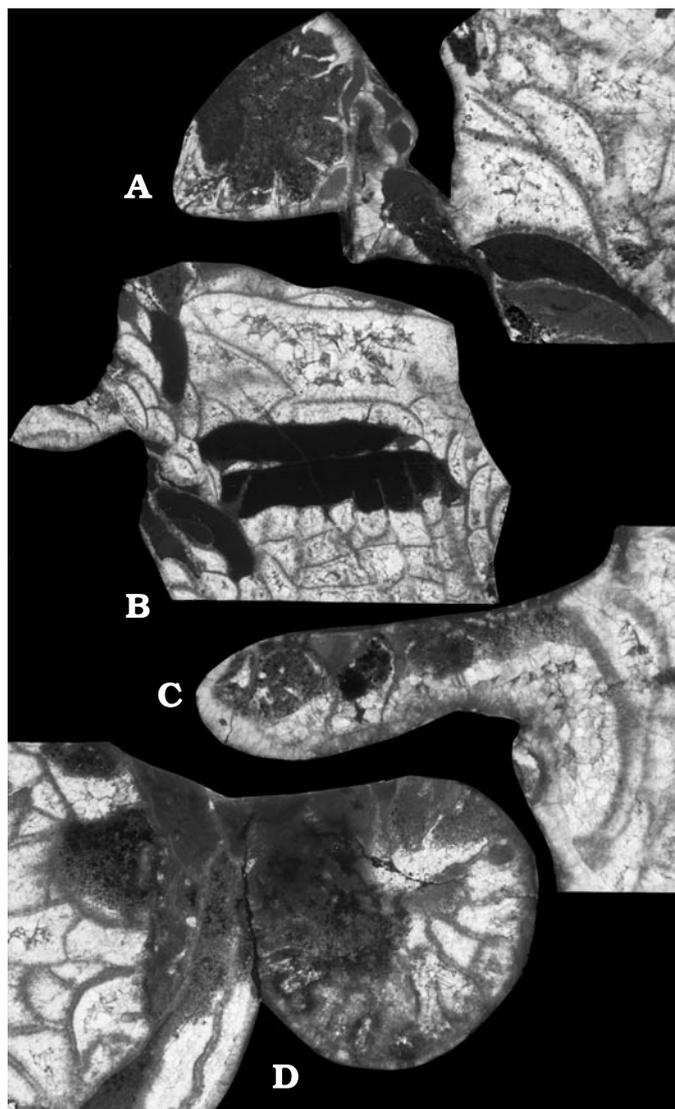

Fig. 5. *Tabulophyllum bonarense* sp. nov. **A**. Cross section DPO 14677b with small offset on left side; × 8.5. **B**. Cross sectionn of corallite DPO 14676. Lateral connecting process on left side; × 4. **C**. Detail of Fig. 4H. DPO 14674. Lateral projection developing from an extension of a lonsdaleoid dissepiment with transverse partitions internally; × 9. **D**. Lateral offset of corallite DPO 14673; × 8.5. All specimens from the Upper Emsian of Colle.

responsible for improving corallite stabilisation, as those structures generally lead to a broadening of the corallite surface in specimens lying on the sea-floor (Fig. 3D), preventing them from sinking into the soft substrate. These structures are very similar to the "connecting processes", which are lateral projections or connecting tubules, described mostly from phaceloid or dendroid rugose corals, like the Devonian genus *Acinophyllum* McLaren, 1959 or the Silurian *Aphyllum leptostylum* Munson and Jell, 1999. Such connections do not imply a direct connection of the soft body of the organism and in most cases stability of the aggregate is only supported by buffer-like projections, as it is the case of *Acinophyllum segregatum* (Simpson, 1900) (Oliver 1976: pl. 21: 2, 6). As the processes in the specimens from Colle (Figs.
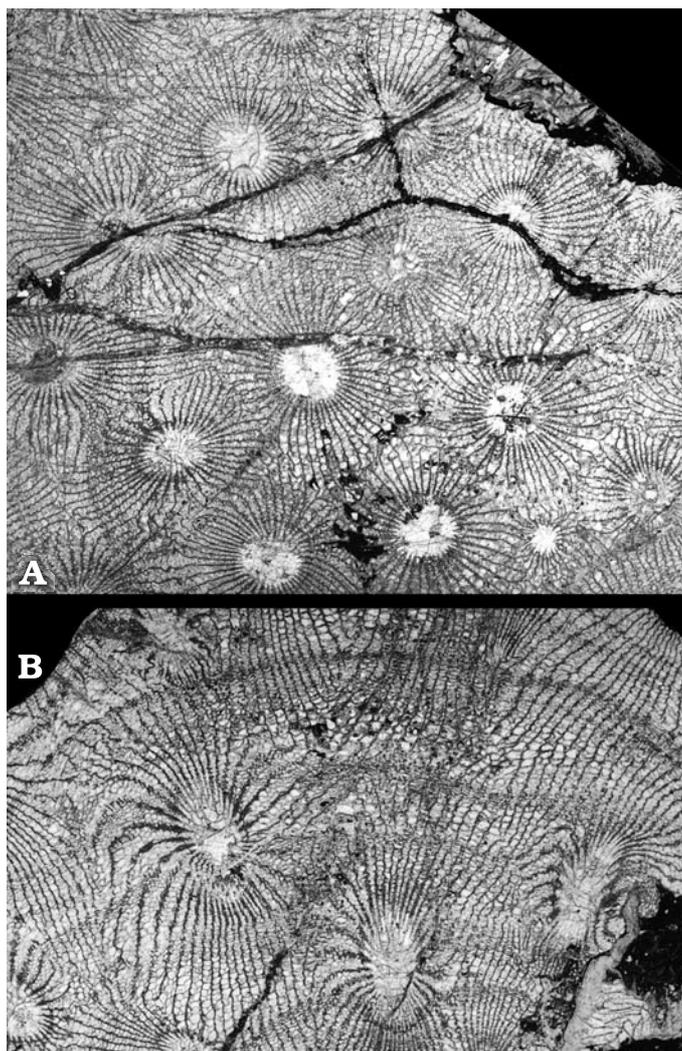
Fig. 6. *Cantabriastraea cantabrica* gen. et sp. nov. **A**. Cross section of holotype DPO 14780. **B**. Longitudinal section of the same. Both × 2. Specimen from the Upper Emsian of Colle.

4F, I, 5B) are very incomplete, it is difficult to decide if they acted as attachment structures or as roots. Although fragments of crinoids are very common in the sediments of the Coladilla Formation at Colle, there is no proof that those corals were attached to articulated crinoidal stems or bryozoan fragments, which is known of some Carboniferous corals from northern Spain (Kullman and Rodriguez 1994).

Family Disphyllidae Hill, 1939
Subfamily ?Paradisphyllinae Jell, 1969

Remarks.—The Paradisphyllinae are a group of predominantly Lower Devonian corals which include genera characterized by fine monacanth septal trabeculae, arranged in a fan like system because of their slightly everted calices (Hill 1981: F271). The subfamily is further defined as a group of genera with fusiform or carinate septa and steeply arched dissepimentarial floors (Jell 1969: 67) and was separated from the Disphyllidae because of their upward spreading trabeculae. The closely related Hexagonariinae are separated by their arrangement of monacanth trabeculae, which show a half-fan in longitudinal section and a different calice morphology, which is not strongly evert. The taxonomic value of external- or calice-forms of corals is generally regarded as not very high, and the proposed separation of a subfamily based on differences in external morphology is therefore questionable (Sorauf 1994). Although carinae are highly variable in the Paradisphyllinae they are usually developed as yardarm-like structures. Some species show only slightly carinate or peripherally incomplete septa of swollen trabeculae, which may give an impression of constituting a string of pearls. A thorough revision of the Hexagonariinae and discussion of their separation from the Paradisphyllinae has been given recently by Sorauf (1994: 333).

Occurrence.—Widely distributed in the Upper Silurian to Middle Devonian of Australia, Western North America, and Asia.

Genus *Cantabriastraea* nov.

Type species: *Cantabriastraea cantabrica.*

Diagnosis.—Astreoid to thamnasterioid genus of the Paradisphyllinae with everted calice and smooth to heavily carinate septa. Septa typically dilated (occasionally spindle-shaped) in the inner dissepimentarium. Carinae irregular, with development of retiform septa towards their peripheral part. Tabulae usually complete and arched.

Remarks.—Some protocorallites of *C. cantabrica* having only slightly thickened and weakly carinate septa (Fig. 8H) bear a strong resemblance to species of the genus *Cyathophyllum* Goldfuss, 1826 (*sensu* Birenheide 1963) and are reminiscent especially of the recently described *Platysmatophyllum* Pedder, 1998, which is known from the Lower Devonian (Emsian, *nothoperbonus* zone) of Cabriéres/Montagne Noire. Although the generic description of *Platysmatophyllum* is based on two specimens only it is regarded as a solitary taxon of the Cyathophyllidae characterized by lateral budding and everted calices. Indeed, septa are very thin even in the inner dissepimentarium (Pedder 1998: fig. 8) and their general morphology is closely similar to *Cyathophyllum*. According to that author, the slightly withdrawn major septa and consequently more complete tabulae in the type species, *P. halleri* Pedder, 1998, are sufficient for separating the genus from *Cyathophyllum*. But such a morphology is not unusual in species of *Cyathophyllum* known from the Eifelian of the Eifel, as in *C. spongiosum* (Schulz 1883). *Cantabriastraea* displays some characters typical of the Cyathophyllidae, like the very thin septa which are carinate and strongly retiform towards the periphery (Fig. 8J). However, as septa within the inner part or the dissepimentarium are generally affected by trabecular thickenings (Fig. 9C) and sometimes by additional stereome, indicating a coarse trabecular structure we regard it as a disphyllid and assign it tentatively to the Paradisphyllinae.

Superficially the new genus also shows some characters diagnostic of *Kuangxiastraea* Yu and Kuang, 1983. Growth

form of both genera is thamnasterioid-astreoid and there are strongly carinate septa with a tendency to retiform degeneration at the periphery, which has been clearly refigured recently in specimens of the type species *K. elegans* from the Upper Givetian of Guangxi (Yu 1997: pl. 1: 3). *Kuangxiastraea* differs from *Cantabriastraea* by its more consistently carinate septa, which are predominantly composed of yardarm carinae. Even if the septa are strongly thickened the carinae are always typically developed as yardarm carinae and zigzag carinae are very rare. Although *Cantabriastraea* is likewise characterized by peripherally retiform septa, its septa bear almost exclusively zigzag carinae. Another difference are the strongly everted calices, causing an arrangement of dissepiment layers in strongly arched series, which is followed by the trabeculae (Fig. 9A). Tabulae are usually complete and arched. The tabularium of *Kuangxiastraea* is composed of incomplete, strongly arched tabellae but the solid axial column/plate consisting of joined distal ends of major septa as observed in the type species by Yu (1997: 270) is most probably not a true axial structure. Another aspect is the difference in the stratigraphic distribution of both genera: whereas *Cantabriastraea* is only known from the Lower Devonian, *Kuangxiastraea* and related genera are widely distributed in upper Givetian and lower Frasnian strata. The Eifelian records of the genus (He 1978) are questioned by Yu (1997: 267) who regards *Kuangxiastraea* as a (regional) index fossil for the Upper Givetian. Several specimens described from the upper Givetian of western Europe and Canada support this assumption (Coen-Aubert 2002; Errenst 1993; Küster 1987). In any case, the two Eifelian species *Kuangxiastraea breviseptata* (Cao in Cao and Lin 1982) and "*H. filata*" *sensu* He, 1978 *non* Schlotheim differ strongly from the new species.

Hillastraea Brownlaw and Jell, 1997 from the Frasnian of NW Australia (Lennard Shelf) was proposed for solitary and thamnasterioid corals with slightly everted calices and strongly naotic septa with presumably compound trabeculae, that appear to be extremely thickened. Tabularium of the type species *H. floriforme* (Hill, 1936) is composed of small, slightly convex tabellae. The classification of *Keriophylloides* Soshkina, 1951 is still unresolved as the trabecular structure of its type-species *K. astreiforme* (Soshkina, 1936) from the Eifelian of the Ural Mtns. is insufficiently known. The species is also characterized by everted calices and strongly carinate/vesiculate (vepreculate?) septa (Soshkina 1936: 62, figs. 71, 72). However, some authors have discussed a possible development of horseshoe-dissepiments in the type specimen and the genus is currently regarded as a phillipsastreid (Hill 1981: F282, Brownlaw and Jell 1997: 333) and questionable synonym of the Australian genus *Bensonastraea* Pedder, 1966. The only other known thamnasterioid-astreoid genus within the Paradisphyllinae is *Radiastraea* Stumm, 1937, which occurs in the Lower Devonian of North America and Australia. It is distinguished from *Cantabriastraea* by having a differently structured tabularium, with a weakly developed axial structure and generally complete septa.
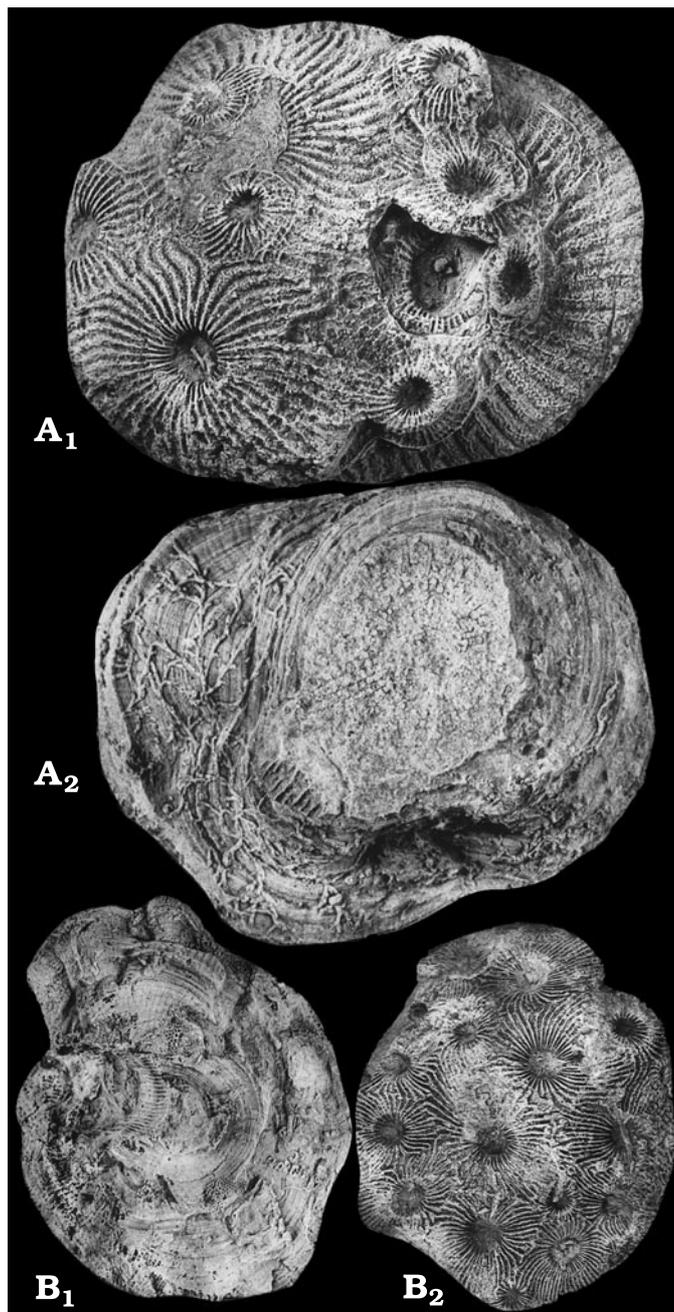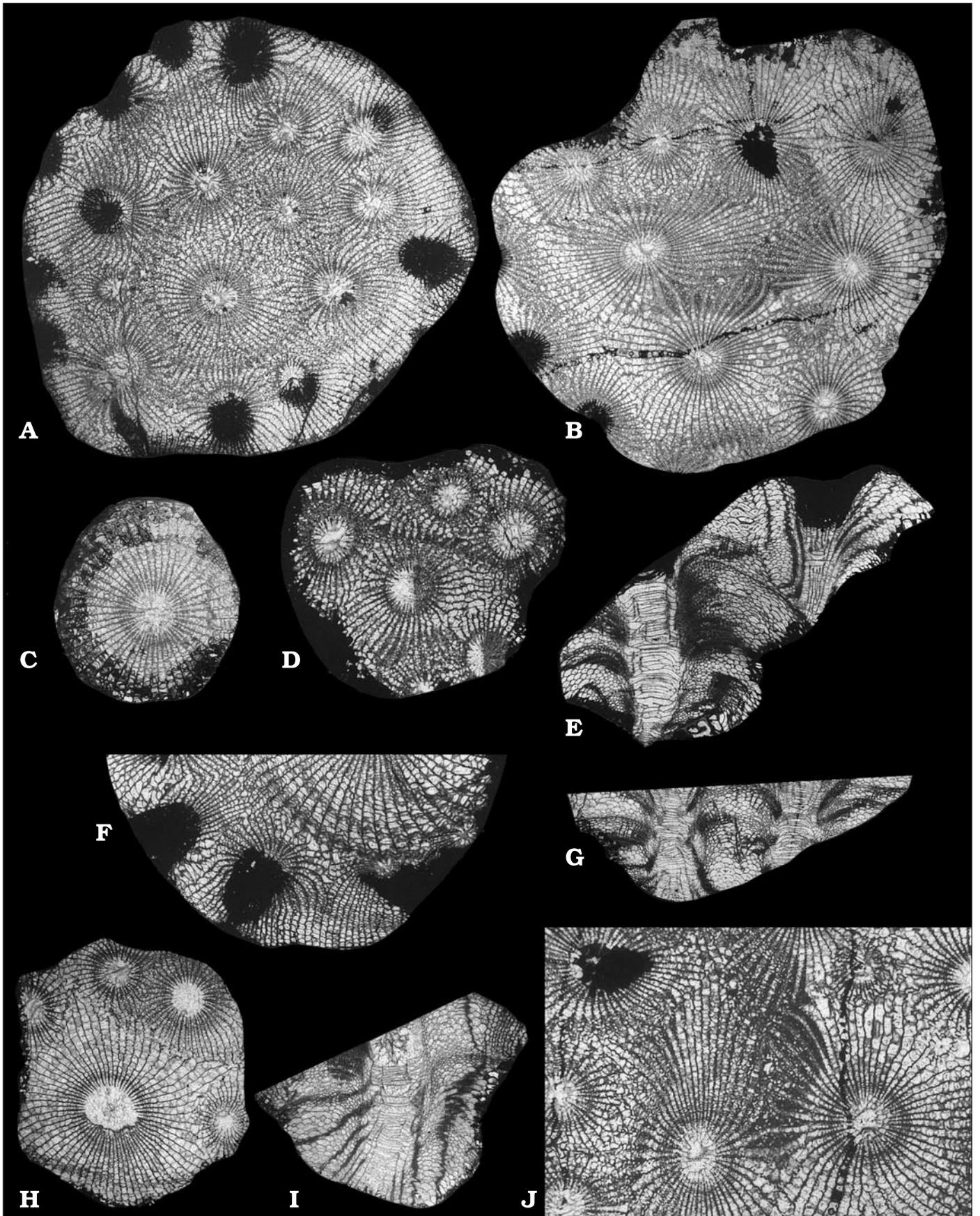

Fig. 7. *Cantabriastraea cantabrica* gen. et sp. nov. **A**. Colony DPO 14811 consisting of a large protocorallite disrupted by nonparricidal, marginal increase in distal view (A_1); septa appear as broad and flat ridges which are strongly retiform towards the periphery. Underside of the same colony (A_2), partly encrusted by *Aulopora* sp.; × 2. **B**. Colony DPO 14813. B_1. Colony underside showing a single protocorallite turned to the left. B_2. Upper surface of the same colony; × 1. All specimens from the Upper Emsian of Colle.

Occurrence.—Lower Devonian (Emsian) of the Cantabrian Mountains (Spain).

Cantabriastraea cantabrica gen. et sp. nov.

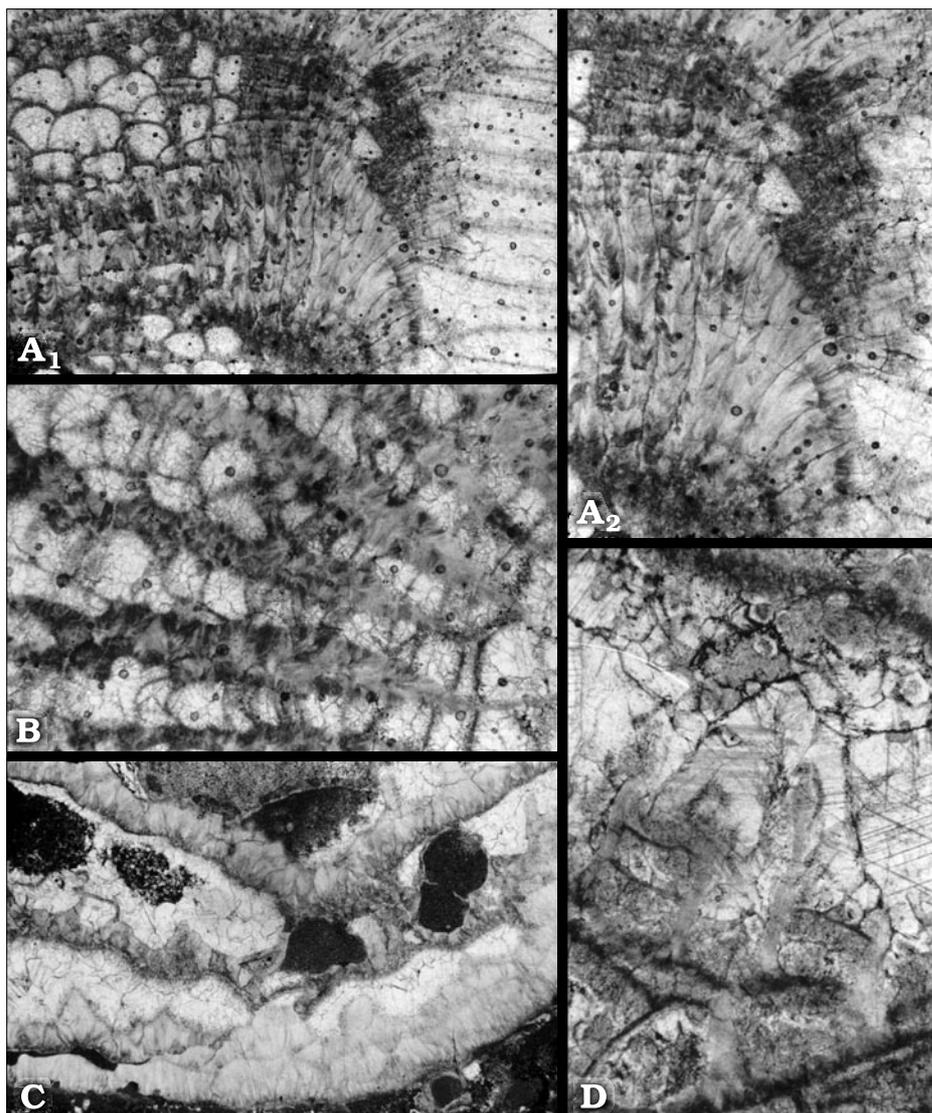Figs. 6A, B, 7A–D, 8A–J, 9 A–C.

Holotype: DPO 14780 (Fig. 6).

Fig. 9. **A**. *Cantabriastraea cantabrica* gen. et sp. nov., specimen DPO 14789. A_1. Cross section of tabularium and inner dissepimentarium. Trabeculae are oriented perpendicular to the rows of dissepiments; × 15. A_2. Detail of A_1; trabeculae intercalate between existing ones or bifurcate; × 20. A_3. Septa in cross section with strong dilations in inner dissepimentarium caused by thickening of trabeculae. Towards the periphery (left side) septa become irregular carinate and may split into discrete trabeculae; × 24. **B**, **C**. *Tabulophyllum bonarense* sp. nov. **B**. Wall of corallite DPO 14673 in cross section. Thickenings of wall and lonsdaleoid dissepiments show a fibrous structure caused by thickened septal bases; × 24. **C**. Thin septa of corallite DPO 14686 (compare with Fig. 4G) inserting on lonsdaleoid dissepiments (dark lines in lower part of picture). Central part towards the axis (top of picture) is strongly affected by cement; × 24. All specimens from the Upper Emsian of Colle.

Type locality: Colle, ca. 5 km SE of Boñar, Province León; Hoja 104 (Boñar), 1°33'37''E/42°50'42''N.

Type horizon: Lower Devonian, Emsian, La Vid Group, upper part of the Valporquero Formation (COL A-1) and lowermost part of the Coladilla Formation (COL B-3).

Derivation of the name: The name derives from the Cantabrian Mountains.

Paratypes: 34 specimens, DPO 14781–14804, 14809–14814, 14828–14830.

Diagnosis.—Type species of *Cantabriastraea* with corallite diameter of 8–13 mm and 19–24 major septa, which do not reach the corallite axis. Diameter of tabularium ranges from 3.5–5 mm. Tabulae complete and slightly arched (13–18 tabulae per 5 mm vertically).

Description.—Coralla are typically small, with a diameter of 5–7 cm at a maximum height of 5 cm and have a distinctive growth form of a flat cake. Small colonies are mushroom shaped and comprise only a few corallites (Fig. 7C), whereas adult colonies typically have a slightly domed surface. Growth starts with the development of a single, cylindrical protocorallite, reaching a maximum diameter of 2 cm (Fig. 8C). This corallite is increasingly replaced by offsets developed by nonparricidal, marginal increase (Fig. 8F, H) and transformed

← Fig. 8. *Cantabriastraea cantabrica* gen. et sp. nov. **A**. Cross section of colony DPO 14789 with medium sized corallites. **B**. Cross section of colony DPO 1790. Corallites are very large and show highly variable development of carinate septa. **C**. Protocorallite of colony DPO 14788. **D**. Cross section of small colony DPO 14783. Septa are strongly thickened especially at dissepimentarium/tabularium boundary. **E**. Longitudinal section DPO 14786. Note strongly arched series of dissepiment-layers and convex tabulae. **F**. Cross section of colony-fragment DPO 14830 with development of juvenile corallites by marginal increase on lower right side of large protocorallite. **G**. Longitudinal section DPO 14790. **H**. Cross section of colony DPO 14787, consisting of a large protocorallite and four juvenile offsets developed by marginal increase. Undilated major septa do not reach to corallite axis. **I**. Longitudinal section of colony DPO 14787. **J**. Corallites of colony DPO 14790 (compare Fig. 8B), with strongly carinate septa breaking down into discrete trabeculae, becoming retiform. A–C, E–I, × 2; D × 3; J × 2.5. All specimens from the Upper Emsian of Colle.

to colonial growth. Apical portions of those protocorallites are not preserved. Some fragments show an attachment to corallite fragments of *Synaptophyllum multiseptatum* Soto, which has obviously been used as hardground. Colony surface is usually well preserved and calices show an everted calicular plane with a deeply depressed and flat central part (Fig. 7A, D). Growth form is astreoid-thamnasterioid, but septa are rarely confluent and limitations of corallites are usually marked by break down of septa. There are no true corallite walls. Calical centres are 8–13 mm apart, but can reach to 17 mm in juvenile coralla consisting of only a protocorallite and few small offsets (Fig. 8H). Morphology of septa is highly variable within a colony as well as in individual corallites. Septa are usually thin near the corallite boundary, but moderately thickened and may bear numerous irregular carinae or lateral spines (vepreculae) in their middle part (Fig. 9C). Close to the dissepimentarium boundary they are usually strongly thickened and may be in lateral contact (Fig. 8D). Carinate septa show a strong tendency to break down into discrete trabeculae giving septa a spongy, retiform morphology. Isolated groups of trabeculae are usually connected by numerous sections of lateral dissepiments, which gives the impression of very broad septa (Figs. 7A, 8J). Trabecular thickening of septa (Fig. 9C) increases towards the tabularium border where they are flanked by numerous coarse carinae. However, there are colonies or corallites with very weak or even smooth septa, which are not affected by any septal degeneration (Fig. 8H). Particularly septa in corallites of small colonies and protocorallites (Fig. 8C) are weakly carinate. Major septa vary from 19–24 in number, but can reach up to 31 in a protocorallite (Fig. 8C). Although there are rhopaloid septa in some corallites, they are generally very slender within the tabularium and do not reach the corallite axis, so that a small axial space of 3.5–5 mm remains free, which is traversed by rare sections of tabulae. Minor septa barely extend into the tabularium. Sections of axially convex dissepiments are numerous, but are increasingly replaced by irregular or lateral dissepiments towards the periphery. Diameter of tabularia ranges from 3.5–5 mm and includes predominantly complete and slightly convex tabulae which are arranged above one another or are supplemented with peripheral tabellae. There are 13–30 tabulae/cm corallite length. The boundary to the dissepimentarium is characterized by steeply inclined globular dissepiments and according with the everted calice, the dissepimental layers are strongly arched (Fig. 8E, G). They are commonly traversed by fanning monacanth trabeculae, which are arranged perpendicular to the dissepiments and may show bifurcations (Fig. 9A, B).

Occurrence.—Only known from the type locality.

Conclusions

Two taxa of Lower Devonian rugose corals from the Cantabrian Montains are described, representing some new faunistic data to the insufficiently known Emsian coral fau-nas of Europe. Both show some unusual features of growth form, which are usually regarded as adaptations to their environment and especially substrate. Adaptation to soft, muddy sediment requires mechanisms of stabilisation like rhizoid structures known from *Tabulophyllum bonarense* sp. nov. or the development of an unusually long lasting protocorallite in *Cantabriastrea*. Some of these protocorallites were attached to bioclasts (*Synaptophyllum* fragments), stabilizing the coral as such. In later stages a flat or mushroom-shaped morphology developed, preventing the colonies from sinking into the soft substrate. A comparable growth form is known from the Frasnian *Hexagonaria buxutiensis* Tsien, 1977, but it is not yet known why numerous other forms living under similar ecological conditions (*Phillipsastrea* species) do not develop such large and long lasting protocorallites. It cannot be refuted that such a growth form must to some extent be genetically controlled and may not only be explained by ecophenotypical response to environmental factors. Because of its unusual "quasi-colonial" growth, *Tabulophyllum bonarense* sp. nov. has shown problems of generic assignment and in this connection a reevaluation of several strongly budding solitary forms related to *Tabulophyllum* is needed.

Acknowledgements

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