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# Earliest Pragian (Early Devonian) corals and stromatoporoids from reefal settings in the Cantabrian Zone (N Spain)

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**ABSTRACT**

The oldest reefal episode in the Cantabrian Zone (earliest Pragian) consists of small biostromal patch reefs, mainly built by corals and stromatoporoids, and developed on a storm-dominated ramp. Four outcrops provide the stratigraphic framework in which these reef facies developed, and these permitted an interpretation of their depositional setting in terms of a relatively distal or protected shelf. We systematically describe three species of rugose corals, five species of tabulate corals, and six species of stromatoporoids. This fauna is allocated to three Pragian fossil associations. Association 1 is mainly composed of massive tabulate corals and stromatoporoids. Association 2 contains dominant branching rugose and tabulate corals. Finally, association 3 is represented by tiny massive tabulate corals. Each association occurs at a specific location within a framework of high-frequency deepening upward cycles, being related to a specific depositional setting. This mode of occurrence suggests that their development was tuned by relative base-level oscillations, forming during rises that took the sea-bottom to relatively deep or sheltered conditions, with rare reworking by storm-related currents. Finally, a comparison of this reefal fauna with examples of similar age from elsewhere is presented in order to explore their affinities.

***KEYWORDS*** **Reefs. Corals. Stromatoporoids. Stratigraphy. Early Devonian. Cantabrian Zone.**

## INTRODUCTION

The Cantabrian Zone (Fig. 1) represents the external belt of the Variscan Iberian Massif in the northwestern Iberian Peninsula. During Early Devonian, the Iberian Massif formed part of the northern flanks of the Gondwana plate, and the area of study was at approximately 35º-40º latitude south (Golonka, 2002). The Devonian record of the Cantabrian Zone comprises an alternation of calcareous and siliciclastic units, with the former containing abundant reef deposits that may be grouped into seven main reefal episodes (Fig. 2). These reefal episodes have been the subject of several stratigraphic and palaeontologic studies (see Méndez-Bedia et al., 1994; Fernández et al., 2006; and references therein).

The earliest reefal episode in the Cantabrian Zone occurred during the early Pragian (Krans et al., 1980). Because of its local occurrence, poor development, and the scarcity of suitable outcrops, this episode has not been studied in detail to date. Thus, the main aim of this paper is to describe the stratigraphy, depositional setting, main reef-building organisms and fossil assemblages of the Pragian strata in the Cantabrian Zone.

Only four sections of this first reefal episode are suitable for study. In these sections, the reef facies begin some metres above the Lochkovian/Pragian boundary, which has been provisionally placed at the first appearance of the brachiopod *Vandercammenina sollei* and the conodont *Caudicriodus angustoides castillianus*. These Pragian structures consist mainly of small biostromal patch reefs. They grew as a result of the baffling and binding activity of several kinds of builders, mainly rugose corals, tabulate corals and stromatoporoids.

Due to regional or global sea-level lowstand, Early Devonian reefs were generally of limited extent and, during the Lochkovian and early Pragian, they were centred on Laurentia and the Ural sealanes flanking Siberia or Baltica (Copper, 2002, fig. 5). Because of the scarcity of reef deposits in the north Gondwana region during the Pragian, obtaining detailed information about these Cantabrian reefal deposits supplements our knowledge of global reef distribution. Comparable early Pragian reefs occur in southern Spain (Ossa-Morena Zone, Rodríguez et al., in press), in western France (flanks of Massif Armoricain, L'Armorique Formation, Pelhate and Plusquellec, 1980) and in Czech Republic (Bohemia, Upper Koněprusy Limestone, Chlupáč, 1967). Pragian reefs were also present on the southern flanks of Laurentia at the time, on the opposite side of the Rheic Ocean.

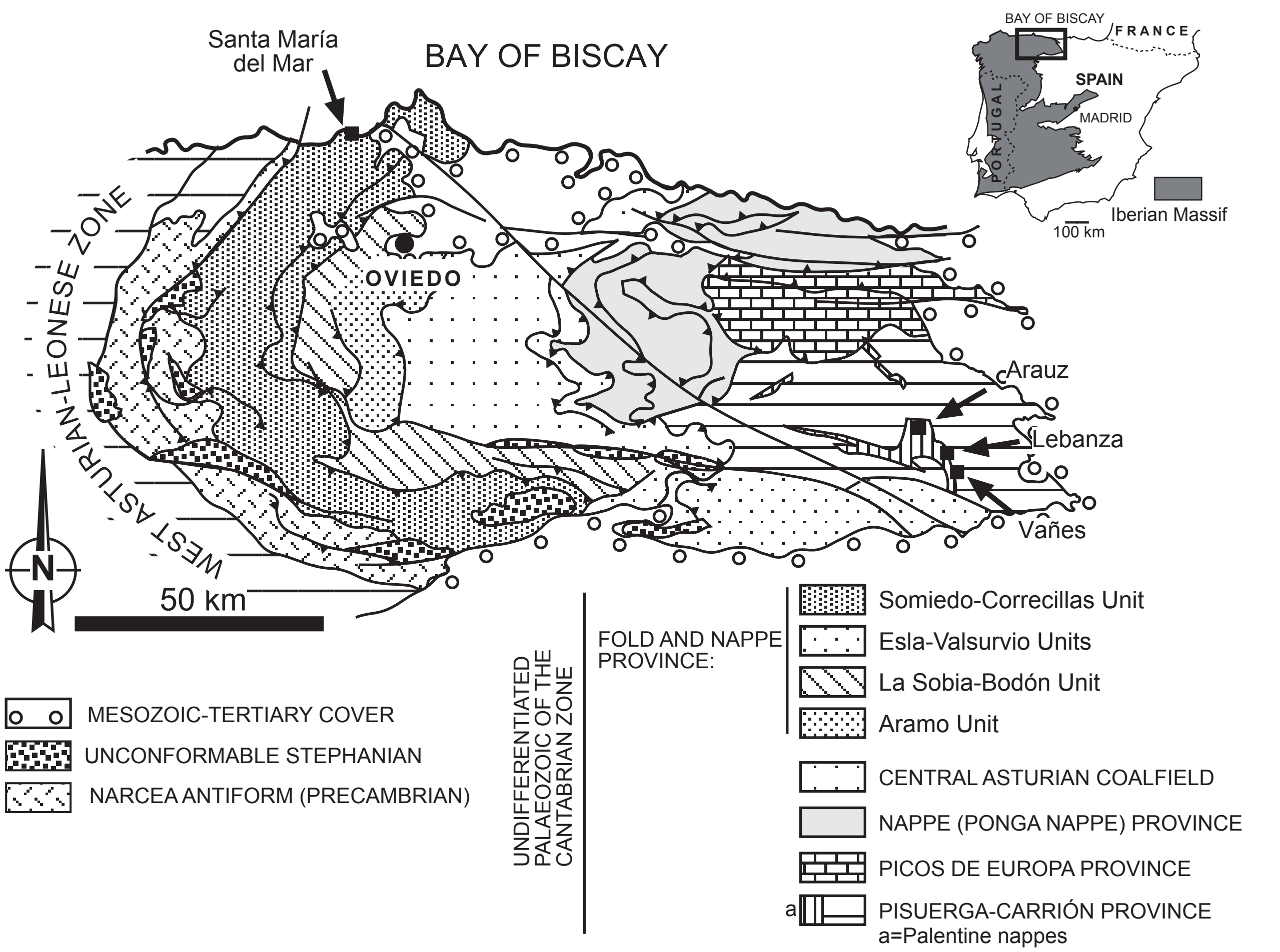


FIGURE 1 | **Geological map of the Cantabrian Zone (modified from Pérez-Estaún et al., 1988) showing the main geological regions and the location of the sections described in this paper. One of these sections (Santa María del Mar) is situated in the northern part of the Cantabrian Zone, belonging to the Fold and Nappe Province; the other three sections (Araúz, Lebanza and Vañes quarry sections) are situated in the southeastern part, in the Pisuerga-Carrión Province.**

## GEOLOGICAL SETTING

From the Cambrian to the Devonian, and prior to the onset of the Variscan orogeny during the Carboniferous, the Cantabrian Zone was a predominantly shallow marine area on the northern passive margin of Gondwana, with mixed sedimentation formed by carbonates and by siliciclastics fed from the Ebro massif, a continental landmass located to the east and north in present-day coordinates (e.g. see Ribeiro et al., 1990; Aramburu et al., 2004). During Devonian times, siliciclastic shelves alternated with carbonate platforms, mainly of the ramp type (Keller, 1997; Vera de la Puente, 1989; Fernández et al., 1997, 2006; Hofmann and Keller, 2006). Sedimentation was governed by regional tectonic and eustatic factors (e.g. see Keller, 1997; Fernández et al., 2006; Hofmann and Keller, 2006; amongst others).

The Devonian rocks of the Cantabrian Zone formed two types of successions, the so-called Asturo-Leonese and Palentine facies, (Brouwer, 1964), which crop out in the Fold and Nappe Province and in the Palentine nappes of the Pisuerga-Carrión Province (Figs. 1 and 2). These two facies were deposited at different locations in the Devonian basin. The succession with Asturo-Leonese facies is shallow-water, in contrast to the Palentine facies, which shows features suggestive of deposition in more distal, deeper areas of the sedimentary basin. The Palentine nappes have been interpreted as Variscan allochthonous units, which were emplaced gravitationally in the Pisuerga-Carrión Province from the south during the Carboniferous (see Rodríguez Fernández and Heredia, 1987 and references therein).

The first episode of carbonate sedimentation began during the middle Lochkovian and is represented by three laterally equivalent units, the middle Lochkovian-Pragian Nieva Formation (Rañeces Group) and the middle Lochkovian-lower Emsian Felmín Formation (La Vid Group), which belong to the Asturo-Leonese facies, and the middle Lochkovian-lower Pragian Lebanza Formation, which belongs to the Palentine facies. The first reefal episode occurred during the earliest Pragian, and is represented by some thin biostromal intervals with a rich fauna of corals and stromatoporoids, from the Nieva and Lebanza Fms. The dolomicritic Felmín Fm., almost devoid of fossils, does not record this first reefal episode.

Here some selected sections of the first reefal episode are studied (Fig. 2). Due to outcrop conditions and accessibility, only four sections were suitable. These are the Santa María del Mar section of the Nieva Fm., and the Araúz, Vañes quarry and Lebanza quarry sections of the Lebanza Fm. (Figs. 1 and 2).

## STRATIGRAPHY

### The Nieva Fm. at the Santa María del Mar section

The Nieva Fm. (middle Lochkovian-Pragian) consists of skeletal limestones, commonly with cross-bedding and ripple lamination, which amalgamated to form packages, or alternate with grey mudstones and marlstones forming a large scale coarsening upward cycle (Fig. 3A; Vera de la Puente, 1989). Subordinate intervals with a reefal fauna, mainly corals and stromatoporoids, are present, and result locally in biostromes up to a few metres thick.

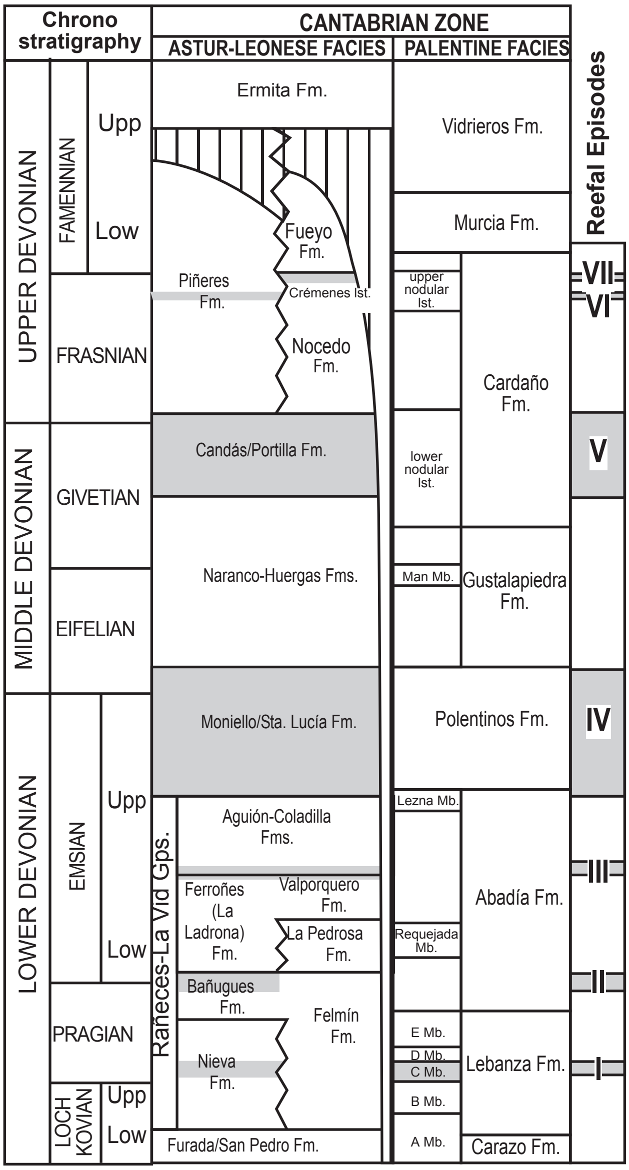


FIGURE 2 | **Chronostratigraphy and lithostratigraphical units of the Cantabrian Zone in both Asturo-Leonese and Palentine facies. Up to seven reefal episodes have been registered in the Devonian rocks of the Cantabrian Zone.**

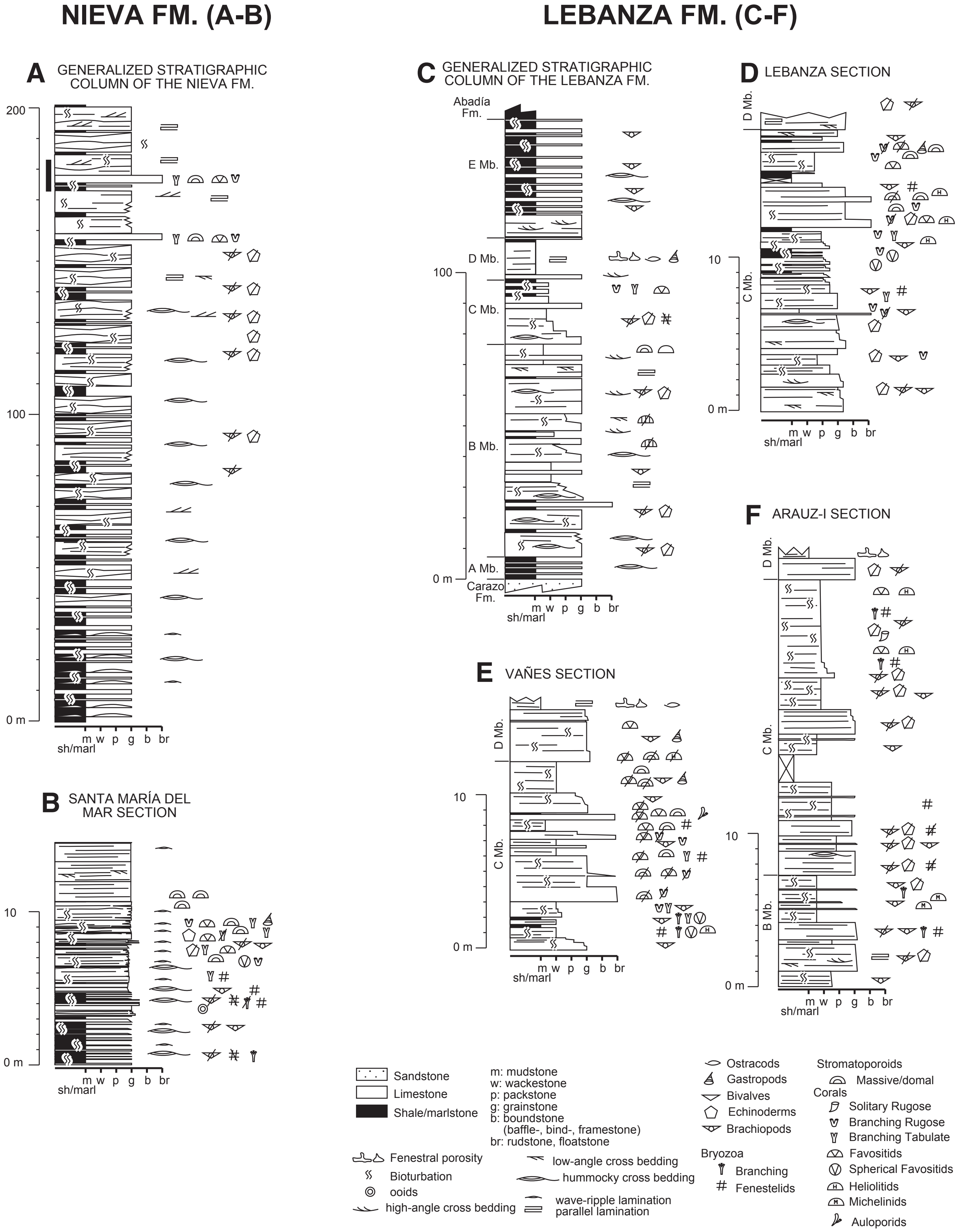


FIGURE 3 | **A) Generalized stratigraphic column of the Nieva Fm. (based on descriptions by Vera de la Puente, 1989). B) Detailed log of the selected interval of the Santa María del Mar section. Its approximate location in the Nieva Fm. is shown by the black bar to the left of the generalized column of A. C) Generalized stratigraphic column of the Lebanza Fm. (based on several sources and our own work), showing the constituent members. D-F) Detailed logs of the selected interval in the sections of Lebanza, Vañes quarry and Araúz (mostly Member C).**

In the Santa María del Mar section (Fig. 1), only the upper part of the formation is accessible since the underlying strata are faulted, or crop out in nearly vertical cliffs. The upper interval of the formation (Fig. 3B) consists of thinly bedded alternations of rippled and hummocky cross-bedded, fine-grained skeletal lime pack- to grainstones and burrowed, fossiliferous grey marlstones and mudstones containing laterally discontinuous sand and silt-grade skeletal laminae. Brachiopods and fenestrate bryozoans are common and occur in situ. Variably broken brachiopod shells are also present within limestone beds, in some instances forming a basal lag. Towards the upper part of the section, limestones become more abundant and form amalgamated, metre-thick packages of fine-grained grainstones bound by centimetre-thick, burrowed, fossiliferous marlstone intervals. Skeletons consist of branching rugose and tabulate corals, with scarce, isolated massive favositids, and irregular to laminar stromatoporoids. These occur on top of the limestone beds, and within the marlstones of the alternations in the middle part of the section.

## The Lebanza Fm. at the Araúz, Lebanza quarry and Vañes quarry sections

In the Palentine nappes, the Lebanza Fm. consists of some 150-160 m of limestones with subordinate marlstones and shales (Fig. 3C). Limestones are mainly skeletal grainstones to packstones, which vary from fine-grained grainstones with HCS, or parallel to low angle cross-lamination, to structureless or cross-bedded coarse-grained grainstones and rud- to floatstones with brachiopod shells, or with fragments of corals and stromatoporoids. Subordinate skeletal wacke- to packstones and intraclast-cortoid dark grey limestones also occur. Towards the top, some intervals are formed by lime mudstones and peloidal limestones with fenestral porosity. Five members, from Member A through Member E, have been distinguished in this formation (Fig. 3C; Krans et al., 1980; see also García-López et al., 2002 and references therein), although there is a disagreement as to where to place the member boundaries. Irrespectively of that, members A and B are characterized by HCS fine-grained grain- to packstones with an upward increase of cross-bedded coarse-grained grain- to packstones in Member B. Member C limestones are mainly dark grey and vary from grainstones to wackestones, containing cortoids (Flügel, 1982) and variably micritized bioclasts, intraclasts with rare peloids, oncoids and microbial crusts. Member D comprises lime mudstones and peloidal limestones with fenestral porosity, and finally, Member E consists again of skeletal limestones alternating with marlstones and shales. With the exception of Member D, the remaining members are largely composed of metre- to decimetre-scale fining upward cycles that can be described in terms of two parts (Fig. 3C-F). The lower part consists of a package of amalgamated pack- to grainstone beds, in some instances with a basal rud- to floatstone interval. It passes upwards into an upper part made of either argillaceous wacke- to packstones with marly or shaly interbeds, or marlstones to shales.

Reefal faunas mainly occur in the upper part of Member B and in Member C (Fig. 3C-F). Fossils of the upper part of Member B appear as broken and reworked skeletons in the rud-to floatstones that form the lower part of the above described fining upward cycles. In Member C, reefal faunas are present as fragments in the basal rud- to floatstones of the packages, or as in situ skeletons. In situ corals and stromatoporoids are found on top of the pack-to grainstone packages, or within the overlying wacke-packstone intervals. Some small coral colonies may be found scattered within the marlstones and shales.

## SYSTEMATIC PALAEONTOLOGY

## Material

Specimens and thin sections described in this paper are housed in the Geology Department at Oviedo University, Spain. All mentioned DPO numbers are included in the catalogue of this institution. All specimens described came either from the upper part of the Nieva Fm. in the locality of Santa María del Mar (Asturias province) (Fig. 3A-B), or from Member C of the Lebanza Fm. in the Vañes quarry, Lebanza quarry and Araúz sections (Palencia province) (Fig. 3C-F).

## Rugose corals

**FAMILY Disphyllidae** H**ILL, 1939**

**GENUS** ***Zelolasma*** PEDDER, 1964

***Zelolasma* sp. 1** (Figs. 4B, 5A, B, C)

*Material:* Nieva Fm., Santa María del Mar section, 5 specimens (DPO 14835, 14836, 14839, 14843 and 14844). Lebanza Fm., Araúz section, 3 specimens (DPO 14643, 14644 and 14646). Lebanza Fm., Lebanza quarry section, 5 specimens (DPO 14605 to 14609).

*External features:* The corallum is fasciculate (phaceloid) with very rapidly increasing corallites. Usually, the increase is lateral, but in some instances tabularial (Fig. 4B), with four corallites occupying the parent area (quadripartite budding). Individual corallites are unequal, and up to 20 mm in diameter, with average values 8-10 mm.

*Internal features:* In transverse section (Fig. 5A, C), the adult corallites show about 30 major septa extending slightly over half-way to the axis. The minor septa attain 2/3 the length of major septa. All septa are rather thin. In immature corallites, septa are shorter and extend half-way to the axis.

In longitudinal section (Fig. 5B), dissepiments are small and globose, and are disposed in two (lower part of the corallite) to six series (upper part of the corallite). Outer series are commonly larger with flattish top and vertical inner face. Inner series smaller, more globose and adaxially declined. Tabulae are mostly horizontal to slightly arched or sagging, complete and rather distant (10-14 tabulae/cm), with occasional peripheral inflated tabellae.

*Remarks:* The mentioned features are diagnostic characteristics of the genus *Zelolasma* Pedder, 1964. Species of this genus are common in Early Devonian time (Pragian), from New South Wales (Australia), Tadzhikistan (N Afganistan) and Taimyr (NE Urales). The Cantabrian species differs from the other Early Devonian species mainly in the number and length of septa and the number of dissepimental series. It could be considered a new species of *Zelolasma*, but a more detailed study is needed.

**FAMILY Ptenophyllidae Wedekind, 1923**
**GENUS *Embolophyllum* Pedder, 1967**
***Embolophyllum* sp. 1** (Figs. 5D, E)

*Material:* Nieva Fm., Santa María del Mar section, 2 specimens (DPO 14838 and 14849).

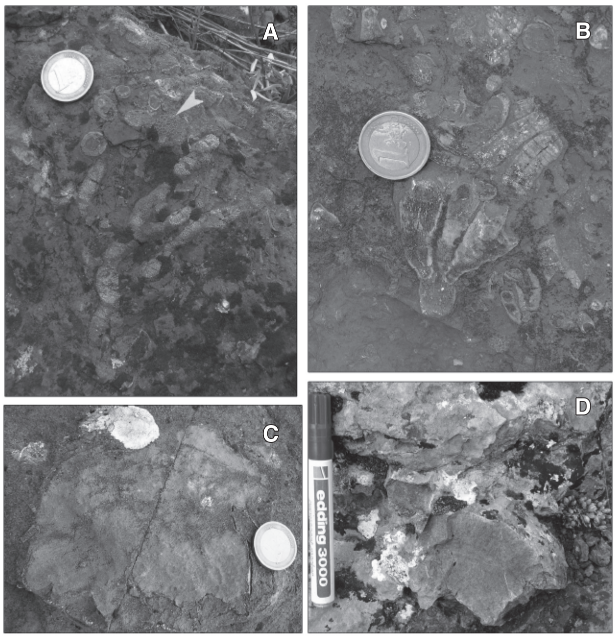


FIGURE 4 | **Outcrop photographs showing some of the fossils described in this paper. A-C (coin's diameter: 23 mm). Lebanza Fm., Lebanza quarry section. A) Coralla of *Thamnopora yavorskyi* Dubatolov surrounded by diverse organisms, including a small *Favosites* aff. *goldfussi* d'Orbigny forma *pyriformis* Lecompte (arrow). B) Small coralla and scattered bioclast of the rugose coral *Zelolasma* sp. 1. C) Natural longitudinal section of *Favosites* sp. D) (permanent marker length: 137 mm). Lebanza Fm., Araúz section. Partly broken stromatoporoid skeleton.**

*External features:* Corallum fasciculate with individual subcylindrical corallites 9-10 mm in diameter. Calices are not exposed in this material, but from the transverse sections it may be assumed that they are funnel shaped (Fig. 5D).

*Internal features:* The peripheral ends of the septa are expanded, so that in transverse section the wall resembles a series of wedges, whose thickness is approximately 0.5 mm. The septa show lateral flanges especially prominent in the tabularium, but they are also slightly carinate in the dissepimentarium (Fig. 5D). The major septa are variable in length: some only just penetrate the tabularium, whereas others extend to the axial region, coiling around the axial ends. Corallites show 28-29 major septa. Minor septa are equally variable and are about two-thirds as long as major septa; normally they do not enter, or only just enter, the tabularium. Septa of both orders may be withdrawn peripherally, especially during later stages of corallite development. Dissepiments vary considerably in size, but inflated (lonsdaleoid type) towards the periphery (Fig. 5E).

*Remarks:* Corallite diameter and number of septa fall within the range of *Embolophyllum asper* (Hill, 1940) and *E. mundum* Pedder, 1967, also of similar age (earliest Pragian). However, *E.* sp. 1 differs from the former in presenting some thicker and more carinate septa, and from *E. mundum* in the inflated dissepiments towards the periphery of the corallite. *Embolophyllum* sp. 1 could be considered as a new species, but scarcity of specimens and lack of young growth stages in longitudinal thin sections suggest open nomenclature.

**FAMILY Tryplasmatidae Etheridge, 1907**
**GENUS *Tryplasma* Lonsdale, 1845**
***Tryplasma aequabile* Lonsdale, 1845** (Figs. 5F, G)

*Material:* Lebanza Fm., Lebanza quarry section, 2 specimens (DPO 14612 and 14615).

*External features:* Solitary, subcylindrical to conical corals, with a maximum diameter of 15 mm, and length ca. 50 mm. Calices are moderately deep, with rather flat axial areas.

*Internal features:* Corallites possess ca. 34-35 major septa extending one-third of the distance to the axis. Septa are acanthine, with thickened spines projected into the calice from the stereoma-thickened wall (Fig. 5G); minor septa are thinner, partially included in the septal stereozone, one-half as long as major septa. Septal dilation peripherally generated a septal stereozone 0.9 mm wide. In longitudinal section (Fig. 5F), tabulae (11-12 per cm) are complete, thin, gently concave, and commonly with

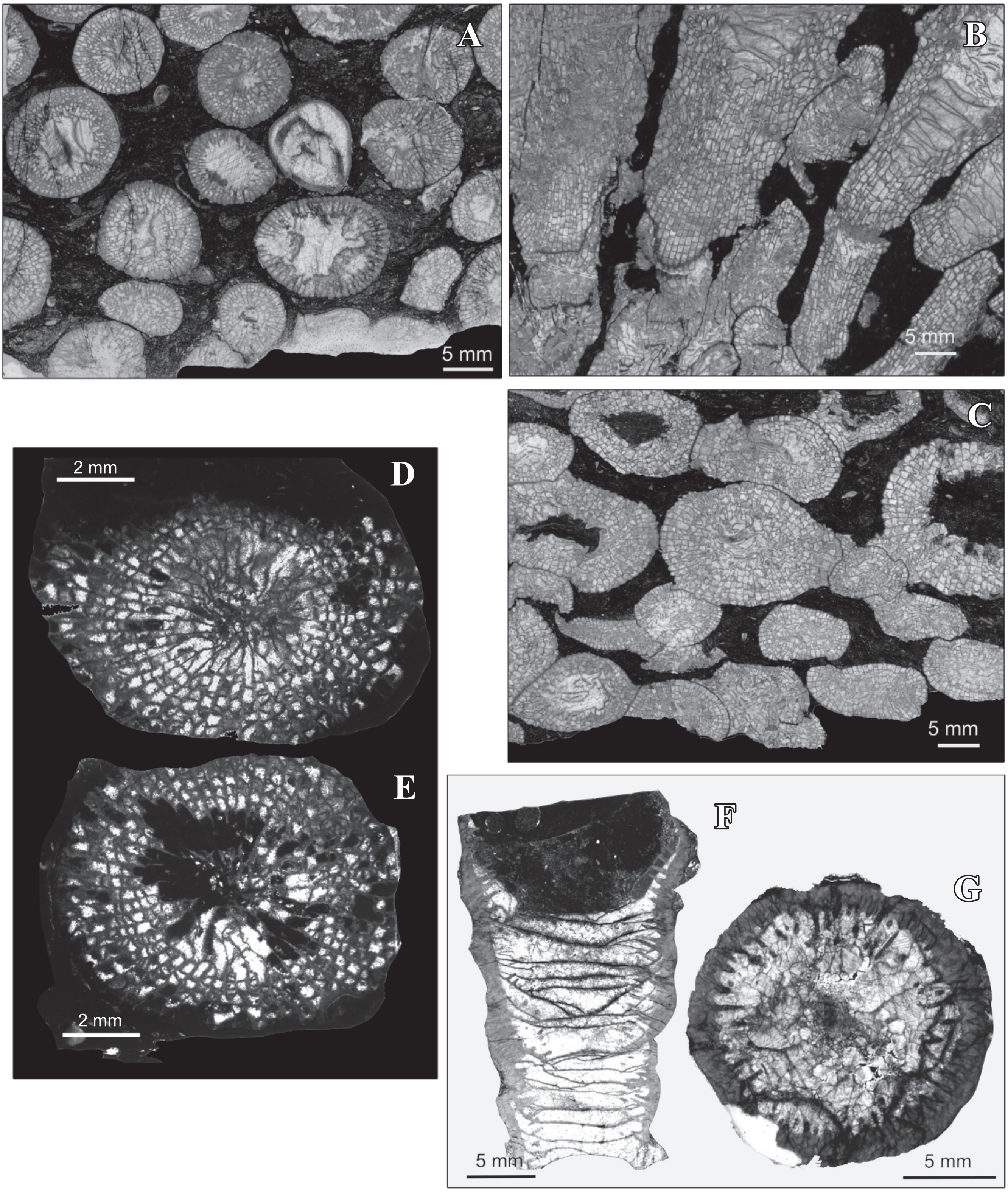


FIGURE 5 | **A-C) *Zelolasma* sp. 1. A) Specimen DPO 14609 (Lebanza Fm., Lebanza quarry section), transverse thin section. B-C) Specimen DPO 14839 (Nieva Fm., Santa María del Mar section), longitudinal and transversal section. D-E) *Embolophyllum* sp. 1, specimen DPO 14849 (Nieva Fm., Santa María del Mar section), transverse sections. F-G) *Tryplasma aequabile* Lonsdale. F) Specimen DPO 14615 (Lebanza Fm., Lebanza quarry section), longitudinal section. G) Specimen DPO 14612 (Lebanza Fm., Lebanza quarry section), transverse section.**

supplementary peripheral tabellae. Microstructure appears rhabdacanthine as in Hill (1981, fig. 7, 1c).

*Remarks:* Corallite morphology, distribution and peculiarities of the different skeletal structures, and measurements fall within the range of variability of *Tryplasma aequabile* LONSDALE, 1845 (see neotype figured by Hill, 1981, fig. 40, 2a-b).

## Tabulate corals

**FAMILY Favositidae DANA, 1846**
**GENUS *Favosites* LAMARCK, 1816**
***Favosites intricatus* POČTA, 1902** (Fig. 6A, B)

*Material:* Lebanza Fm., Vañes quarry section, 3 specimens (DPO 15501-15503) and Lebanza quarry section, 2 specimens (DPO 15504-15505).

*External features:* Coralla have tabular to hemispherical growth forms. They are medium sized, with maximum diameter measured of 8 cm, and height of 6 cm (none sample was complete).

*Internal features:* In transverse section (Fig. 6A), corallites appear as polygons of regular or slightly irregular shape and homogenous size with dimensions between 0.6 and 1 mm (0.58 minimum, 1.07 mm maximum). Walls appear to be thin to moderately thick due to cyclomorphic variations; usually from 0.1 to 0.15 mm thick, but locally 0.3 mm. Wall pores, in 1 or 2 rows, are quite common, commonly with thin, straight pore-plates, and diameters of ca. 0.15 mm; some pore diameters of up to 0.22 mm. In longitudinal section (Fig. 6B), density banding is strongly developed, and marked by variations in wall thickness, distance between tabulae and, especially, in septal apparatus. Spines are very common, usually with circular outline but commonly developed as narrow squamulae in zones with slight cyclomorphic thickening. Tabulae are usually complete, flat or slightly concave or convex, or locally incomplete. Tabular spacing varies between density bands; in low-density bands spacing is ca. 22-32 tabulae per cm; in high-density bands ca. 28-42 per cm.

*Remarks:* The coralla are similar to *Favosites intricatus* POČTA as described by Galle (1978). Cantabrian specimens also show a fairly well developed cyclomorphic zonation (density banding), which Galle (1978) indicated as being a characteristic feature. *F. intricatus* come from the Pragian of Bohemia (Upper Koněprusy Limestone), and is cited from the Early Devonian of the Southern Urals (Zhavoronkova, 1972), and Asian localities (see Galle, 1978; but few citations match *F. intricatus* in detail).

Two similar species are *Favosites alpina* R. HÖRN (in Penecke, 1894) from the Early to Middle Devonian of Graz, which differs slightly in the smaller corallites and in pore disposition, and *Favosites squamuliferous* forma *nitidus* CHAPMAN, 1914 (studied by Philip, 1960), which shows well-developed squamulae.

***Favosites* aff. *goldfussi* D'ORBIGNY forma *pyriformis* LECOMPTE, 1939** (Fig. 6C-F)

*Material:* Nieva Fm., Santa María del Mar section, 9 specimens (DPO 15506-15514). Lebanza Fm., Vañes quarry section, 4 samples (DPO 15515-15518); Lebanza quarry section, 2 samples (DPO 15519-15520).

*External features:* Coralla are usually very small. They have sub-spheroidal, hemispherical and, more rarely, irregular, low, domical growth forms. Size range is ca. 1-2 cm diameter to ca. 8 cm; most coralla are 4-5 cm in diameter and <2 cm high. Two samples from Santa María del Mar section were 12 cm in diameter and 9 cm high, with irregular morphology.

*Internal features:* In transverse section (Figs. 6C, E, F), corallites are polygonal to circular and show heterogeneous size and shape. Large, adult corallites with 7 to 9 sides are usually circular and have diameters of 1.5 to 2.2 mm, and are surrounded by small corallites with 3 to 5 sides and diameters of 0.7 to 1.25 mm. Corallite wall thickness is commonly 0.10-0.12 mm, but varies from 0.05-0.15 mm. Wall pores are distributed in one or two rows, usually with a thin pore-plate, with diameters 0.15 to 0.25 mm. Septa are developed as numerous short spines. Tabulae are regular to very irregular, even vesicular (Fig. 6D); ca. 6-8 tabulae per cm, some 16-18 tabulae per cm. Coralla commonly show a circumrotatory growth pattern (Figs. 6E, F).

*Remarks:* Coralla are characterized by their circumrotatory growth pattern, and by abundant 3-4-sided corallites, probably related to ecological factors. Three other species share a similar growth form and heterogeneity of corallites: *Favosites granulosus* LE MAÎTRE, 1947 from the Emsian of Morocco, *Favosites styriacus* PENECKE, 1894 from the Emsian of the Carnic Alps (reported in the Emsian Cantabrian Zone by Oekentorp, 1975), and *Favosites svagercus* GALLE, 1978 from the Pragian of Bohemia. However, the corallite dimensions of these species are different.

The coralla share several features with Eifelian *Favosites goldfussi* forma *pyriformis* LECOMPTE (1939), including heterogeneous growth in the young stages, and local development of short and numerous spines. The Belgian species shows a regular growth pattern during the adult stage, and has complete, or globose tabulae, but lacks cyclomorphic variation. These features may be ecologic but their persistence in two different geologic sections and different beds precludes assignment to *Favosites goldfussi* forma *pyriformis*.

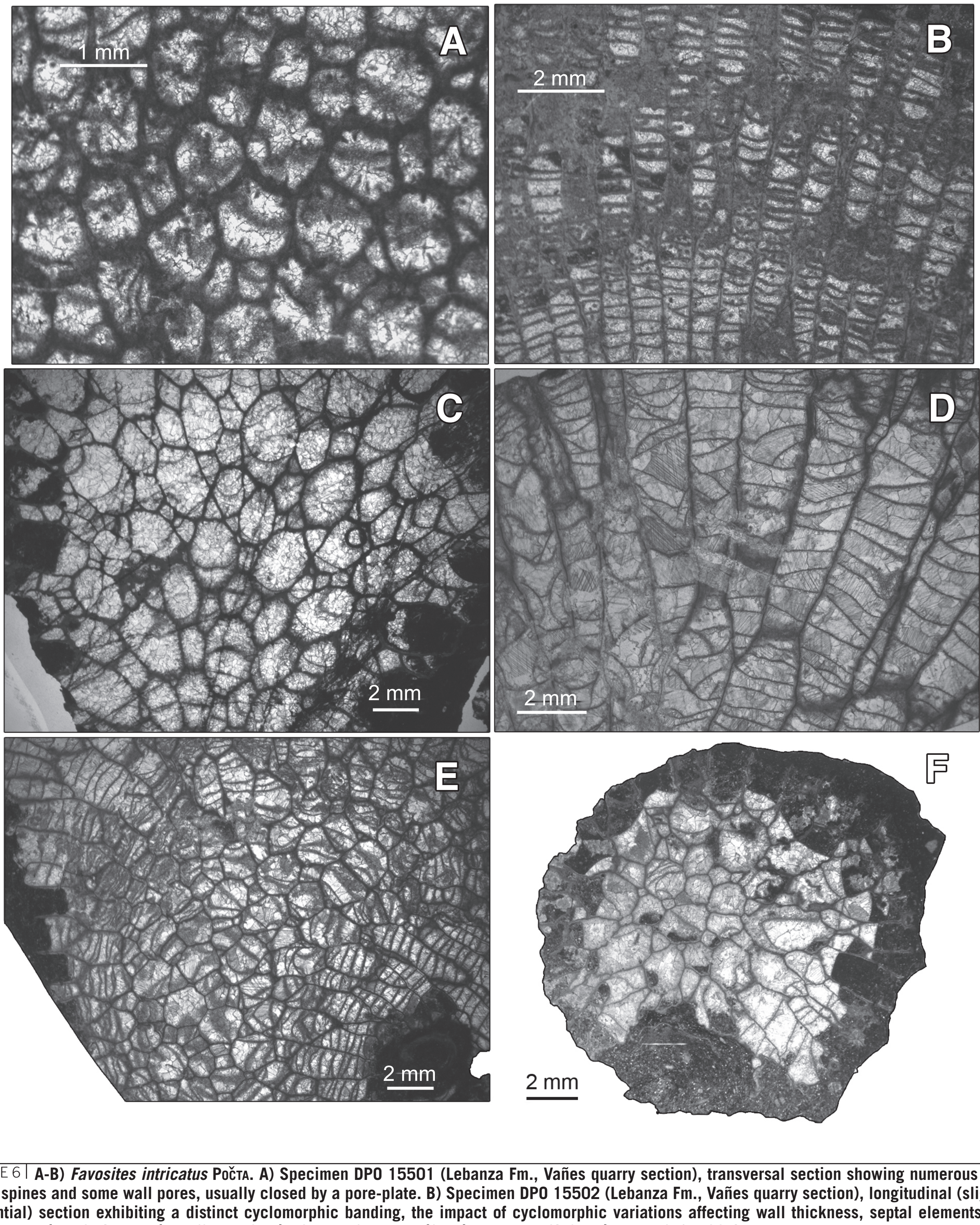


FIGURE 6 | **A-B) *Favosites intricatus* Počta. A) Specimen DPO 15501 (Lebanza Fm., Vañes quarry section), transversal section showing numerous long round spines and some wall pores, usually closed by a pore-plate. B) Specimen DPO 15502 (Lebanza Fm., Vañes quarry section), longitudinal (slightly tangential) section exhibiting a distinct cyclomorphic banding, the impact of cyclomorphic variations affecting wall thickness, septal elements and tabulae spacing. C-F) *Favosites* aff. *goldfussi* D'Orbigny forma *pyriformis* Lecompte. C) Specimen DPO 15520 (Lebanza Fm., Lebanza quarry section), transversal-tangential section showing the heterogeneous pattern of corallite size and shape, and the local development of spines. D-E) Specimen DPO 15510 (Nieva Fm., Santa María del Mar section). D) Longitudinal section exhibiting bent, irregular, even vesicular tabulae; E) Tangential section showing the nearly circumrotatory pattern of growth. F) Specimen DPO 15509 (Nieva Fm., Santa María del Mar section), a small colony with a nearly complete circumrotatory growth.**

Corallum morphology may be strongly controlled by sedimentation. A different life span, as well as episodes of terrigenous mud influx, may explain the presence of two different types of colonies (Gibson and Broadhead, 1989).

**GENUS *Squameofavosites* CHERNYSHEV, 1941**
***Squameofavosites* ex. gr. *cechicus* GALLE, 1978** (Fig. 7)

*Material:* Lebanza Fm., Vañes quarry section, 9 specimens (DPO 15521-15529), and Araúz section, 1 specimen (DPO 15530).

*External features:* Coralla range from low to high domical, and from slightly to highly irregular sub-spheroidal growth forms. Maximum size of coralla is ca.11 cm in diameter and 7 cm high.

*Internal features:* In transverse section (Fig. 7A), corallites are regular or irregular polygons. Corallite dimensions are extremely variable, 1-2.5 mm (exceptionally, corallites reach 2.7 mm). Several exhibit significant heterogeneity, with small 3-4-sided corallites located randomly among adult corallites bearing 6-9 sides. Corallite wall thickness is variable, commonly 0.1 to 0.2 mm, but reaching 0.3 mm in high-density bands (in samples where banding is developed). Wall pores are very common and develop in one or two rows; in the latter, pores are near wall corners; pore diameters are 0.18-0.24 mm. Septa are very common, but in several specimens they were lacking in some places; septa are developed as coarse squamulae, sometimes with long spines. In longitudinal section (Figs. 7B, C), most coralla show significant density banding, with cyclomorphic variation of wall thickness, septal development and tabulae spacing and pattern. Along low-density bands, tabulae are flat or slightly convex and complete, and the number found per cm length varies from 10 to 14. In high-density bands, tabulae are wavy, strongly concave or convex, or even vesicular, and some are incomplete; number of tabulae per cm length varies from 26-30.

*Remarks:* Coralla are assigned to the genus *Squameo–favosites* by significant presence of septa, mainly as squa–mulae, and showing high variability. High intraspecific variation suggests that the coralla are conspecific.

Galle (1978) quantitatively established *Squameofavosites cechicus,* formerly assigned to *Favosites hemisphaericus* var. *bohemica* POČTA (1902) by its different corallite dimensions. The Cantabrian coralla are similar to the Bohemian species, although the pore diameters are slightly smaller. Most of the specimens assigned to *Squameofavosites bohemicus* by Russian authors (Dubatolov, 1959, 1963; Dubatolov and Smirnova, 1964, among others) are quite similar to *S. cechicus,* but with minor quantitative differences.

**GENUS *Thamnopora* STEININGER, 1831**
***Thamnopora yavorskyi* DUBATOLOV, 1959** (Figs. 4A, 8)

*Material:* Nieva Fm., Santa María del Mar section, 25 specimens (DPO 15539-15563); Lebanza Fm., Vañes

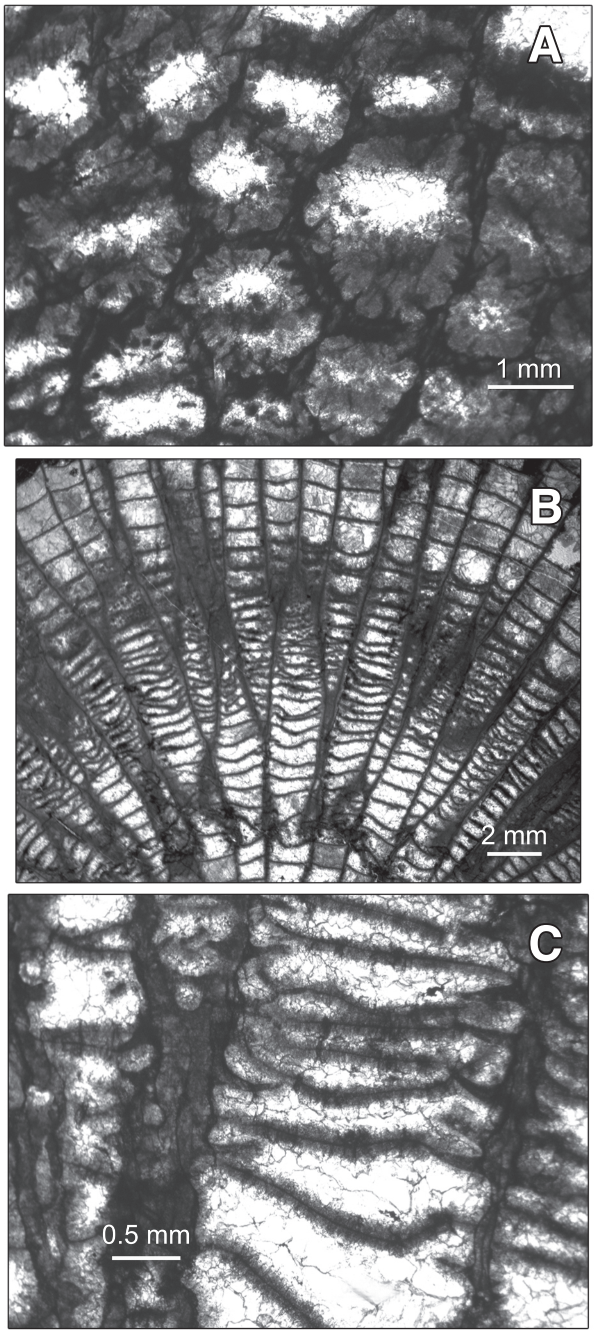


FIGURE 7 | ***Squameofavosites* ex. gr. *cechicus* GALLE. A) Specimen DPO 15525 (Lebanza Fm., Vañes quarry section), transverse section in a high-density band, showing a thick wall, several pores and well developed septa (both squamulae and spines). B) Specimen DPO 15528 (Lebanza Fm., Vañes quarry section), longitudinal section exhibiting a clear cyclomorphic variation of several skeletal elements. C) Specimen DPO 15525, detail of a longitudinal section in a high-density band; note the development of squamulae and their relationship to the tabulae.**

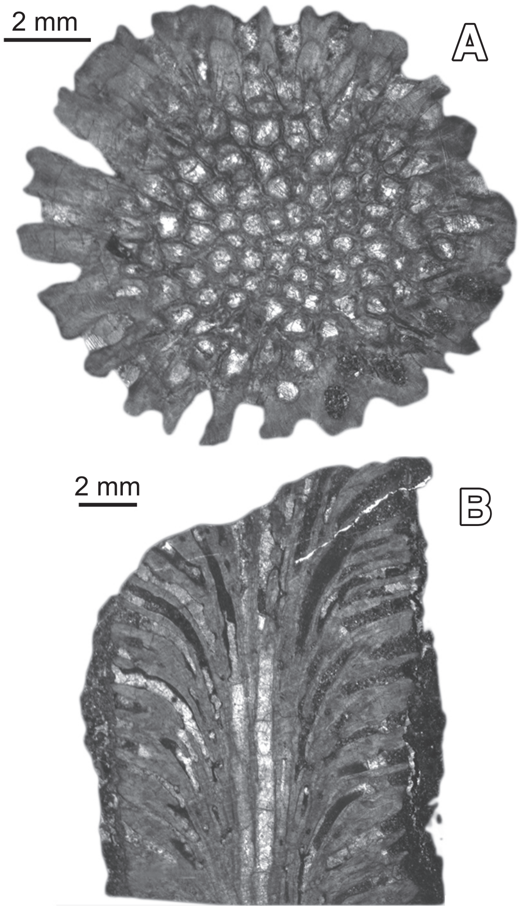


FIGURE 8 | ***Thamnopora yavorskyi*** **DUBATOLOV. A) Transverse section of the specimen DPO 15547, showing a wide axial zone composed of many corallites. B) Longitudinal section of the specimen DPO 15539. Both specimens come from Nieva Fm., Santa María del Mar section.**

quarry section, 20 specimens (DPO 15564-15583), and Lebanza quarry section, 4 specimens (DPO 15535-15538). Several fragments probably belonging to this species have been collected in Araúz section, but they have not been sectioned.

*External features:* Corallum ramose. Branches cylindrical or slightly compressed, with diameters 6-13 mm, mostly 7-10 mm; diameters of the smallest branches are 4-6 mm. Coalescence between branches occurs.

*Internal features:* The axial zone is wide, composed of many corallites, and surrounded by a usually narrow peripheral region; a wide transitional zone may be developed between these (Fig. 8A). In longitudinal section (Fig. 8B), the axial zone is composed of straight corallites, which are slightly bent near the surface, opening to right angles. In the transverse section of the axial zone, corallites are polygonal in outline but internally rounded; diameters range from 0.4 to 0.8 mm, although mostly 0.6-0.7 mm. Wall thickness is ca. 0.10-0.14 mm in the axial zone, but increases near the surface, reaching 0.35-0.45 mm in the calice. Wall pores are frequent, with diameters of about 0.1-0.14 mm, up to 0.18 mm peripherally. Tabulae are scarce, usually flat, slightly concave or convex, distance between tabulae varies widely ranging from 0.36 to 1.3 mm. Septal apparatus is absent.

*Remarks:* The Cantabrian branches are similar to two species from the Early Devonian of the Kuznetsk basin: *Thamnopora taymirica* (CHERNYSHEV, 1941) has corallites with diameters slightly larger (0.7-0.8 mm), and *Thamnopora yavorskyi* DUBATOLOV matches the Cantabrian material, with the exception of pores, which are slightly smaller in the Russian species.

**FAMILY Heliolitidae LINDSTRÖM, 1873**
**GENUS *Heliolites* DANA, 1846**
***Heliolites* cf. *praeporosus* KETTNEROVÁ, 1933** (Fig. 9)

*Material:* Lebanza Fm., Vañes quarry, 3 specimens (DPO 15531-15533), Lebanza quarry, 1 specimen (DPO 15534).

*External features:* Hemispherical coralla of medium size (maximum size 9x7x5 cm).

*Internal features*: (Figs. 9A-B). Cylindrical tabularia surrounded by coenenchyme composed of prismatic tubules. Tabularia diameters vary from 0.82 to 1.14 mm; the number of corallites per $cm^2$ varies between 36 and 38 (32 and 43 being extreme); tabularia show 12 radial rows of discrete, short spines (but completely lacking in sample DPO 15531). Tabulae are complete and commonly horizontal, although some convex or irregular tabulae are present; their number varies from 16 to 80 per cm, averaging 30 to 60 tabulae per cm. Prismatic tubules show a polygonal outline (4-6 sides), and there are from 1 to 3, rarely 4, tubules between two tabularia. The number of tubule tabulae is very constant, ranging between 20 per cm and 40 per cm.

*Remarks:* Given the cylindrical tabularia surrounded by coenenchyme of prismatic tubules with complete tabulae and 12 rows of septa, this material belongs to the genus *Heliolites* DANA. Cantabrian specimens are comparable to Pragian *Heliolites praeporosus* KETTNEROVÁ from Bohemia (Upper Koněprusy Limestone), but the Bohemian species is characterised by the presence of long spines, only occasionally seen in the Cantabrian specimens possibly due to poor preservation.

The Spanish material is probably synonymous with *Heliolites* cf. *praeporosus*, as described by Galle and Weyer (1972) from the late Pragian of Thuringia. Jones and Hill (1940) regarded *Heliolites praeporosus* (and others from the Silurian and Devonian of Europe) as a synonymous

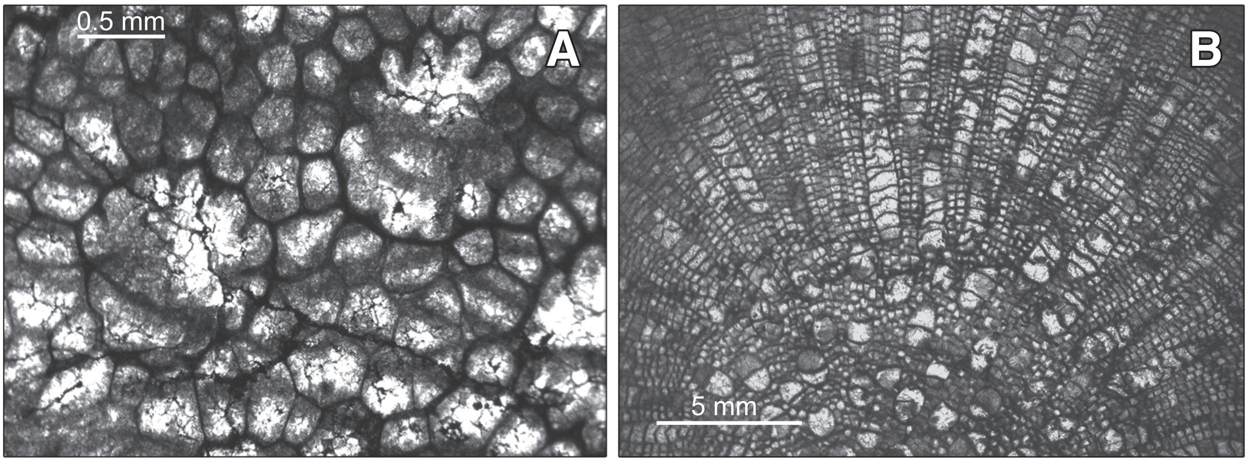


FIGURE 9 | ***Heliolites* cf. *praeporosus* KETTNEROVÁ. A) Specimen DPO 15532 (Lebanza Fm., Vañes quarry section), detail of a transverse section; note the septa, which are partially lost due to recrystalization. B) Specimen DPO 15531 (Lebanza Fm., Vañes quarry section), tangential and longitudinal sections showing diverse types of tabulae. Some weak density bands are developed.**

with *Heliolites daintreei* NICHOLSON and ETHERIDGE, 1879 from the Devonian of North Queensland (Australia). Birenheide (1985) pointed out that *H. praeporosus* is close to *H. tranquillus* GALLE, 1973 from the Acanthopyge Limestone of Bohemia.

## Stromatoporoids

**FAMILY Labechiidae NICHOLSON, 1879**
**GENUS *Labechiella* YABE and SUGIYAMA, 1930**
***Labechiella* sp. 1** (Fig. 10A, B)

*Material:* Lebanza Fm., Araúz section, 2 specimens (DPO 33556-33557).

*External features:* Skeleton undulate, irregular to bulbous, and up to 20 cm in diameter. Most skeletons are moderately latilaminate (2-5 mm thick).

*Internal features:* In longitudinal section (Fig. 10A), cyst plates are elongated and flattened with a tendency to be aligned, resembling laminae, quite commonly wrinkled; in places small cysts of low to moderate convexity occur; cyst plates are irregular in height (0.15 to 0.60 mm) and length (0.30 to 3.6 mm, locally 5-8 mm), spaced 10 to 20 per 5 mm vertically. Cyst walls, commonly very thin (0.03 to 0.06 mm thick), consist of compact tissue. Pillars are well developed, continuous, long (up to 4 mm vertically, but most commonly 1 mm in length), cone shaped, with cone-in-cone outlines and thick (maximum diameter 0.2-0.4 mm); pillars are very irregularly distributed; in some spaced 5 to 10 per 5 mm but in others, very scarce or nearly absent. In tangential section (Fig. 10B) pillars rounded with centre to centre spacing of 0.2 to 1 mm.

*Remarks:* Specimens show the diagnostic characteristics of *Labechiella* YABE and SUGIYAMA, 1930, such as stout and continuous pillars, and flattened cyst plates. Species of this genus are common in the Ordovician, but up to now, only a few are known from Lower Devonian rocks (Webby, 1993; Webby and Zhen, 1997). *Labechiella* sp. 1 shows some resemblance to *L. regularis yizhangensis* LI, 1982 from Upper Devonian-Lower Carboniferous? successions of China, but differs in having less vesicular and more laterally persistent cyst plates, and more widely spaced pillars. This species may also be distinguished from *Labechiella* sp. described by Webby and Zhen (1997) from the Early Devonian (Lochkovian) of Australia by having fairly wrinkled and less horizontally continuous cyst plates, and more convex cysts; pillars in general are shorter. The Cantabrian specimens are unlike known species of this genus, but await more sampling.

***Labechiella* sp. 2** (Fig. 10C-E)

*Material:* Lebanza Fm., Vañes quarry section, 3 specimens (DPO 33558-33560).

*External features:* Skeleton mostly irregular, up to 40 cm across, latilaminae rarely developed; a few low domical, up to 8 cm diameter, with mamelons.

*Internal features:* In longitudinal section (Fig. 10C, E) skeletons consist of rows of large cyst plates, typically flattened and aligned as laminae with variable height (0.27 to 0.60 mm); spacing of cysts ranges from 12 to 17 per 5 mm vertically, their walls, composed of compact tissue, generally thin (0.03-0.06 mm); smaller convex cysts are uncommon. Pillars are continuous and long, usually 1.5 mm in length but up to 7 mm, commonly cone- shaped, with slight cone-in-cone outlines. Pillars are regularly distributed, spaced 7 to 10 per 5 mm and thick (maximum diameter 0.20-0.45 mm). In tangential section (Fig. 10D), pillars rounded, with centre to centre spacing 0.30 to 0.57 mm.

*Remarks:* This form, as the previous, is different to known species of *Labechiella*. It resembles *Labechiella* sp. 1 as regards to pillars, wall thickness and spacing of cyst plates. However, *Labechiella* sp. 2 is clearly distinguished from *Labechiella* sp. 1 by exhibiting more later-

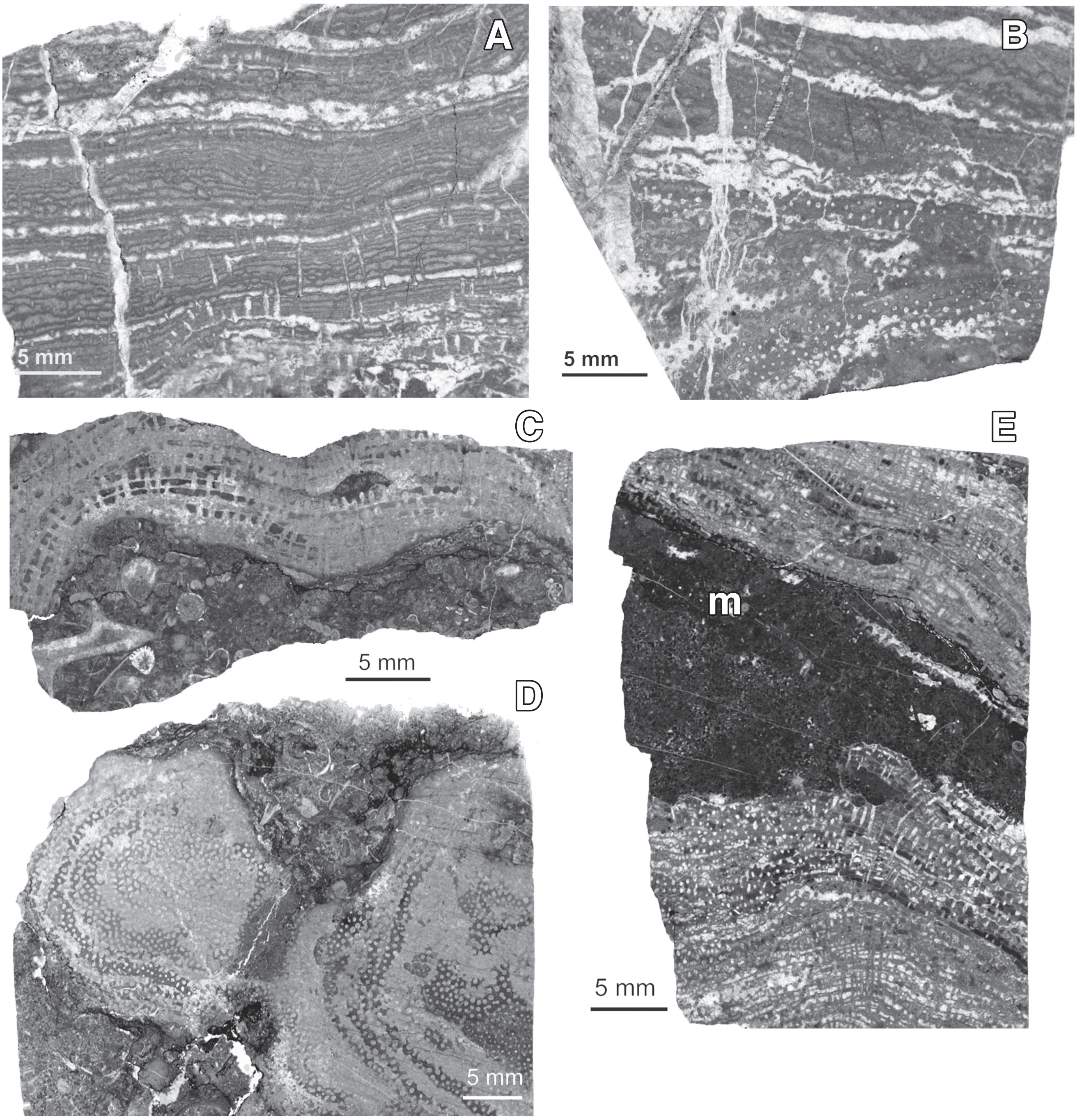


FIGURE 10 | **A-B) *Labechiella* sp. 1. A) Longitudinal section. Specimen DPO 33556 from Araúz section (Lebanza Fm.). B) Tangential section of the same specimen. C-E) *Labechiella* sp. 2. C) Longitudinal section. Specimen DPO 33559 from the Vañes quarry section (Lebanza Fm.). D) Tangential section of the same specimen. E) Longitudinal section, partly oblique, of the specimen DPO 33558 from the same locality showing very long, regularly distributed pillars. Note the microbial micrite (m) with a distinctive clotted appearance within a stromatoporoid margin.**

ally persistent and large, flattened cyst plates resembling laminae, and more numerous and regularly distributed pillars.

**FAMILY Atelodictyidae Khalfina, 1968**
**GENUS *Intexodictyon* Yavorskii, 1963**
***Intexodictyon perplexum* Yavorskii, 1963** (Fig. 11A, B)

*Material:* Nieva Fm., Santa María del Mar section, 5 specimens (DPO 33551-33555).

*External features:* Skeletons are mostly flattened, bulbous or undulate, about 20 cm in diameter; others are laminar and irregular, up to 4 cm thick and 80 cm in diameter.

*Internal features:* Longitudinal sections (Fig. 11A) display variations in the skeletal tissue with inconspicuous phases limited by a basal growth zone of irregular tissue (1-2 mm thick), with a crescent development in places. Skeletons show primary and additional laminae, locally developed, in interlaminar spaces; primary laminae are dark, thin (0.03 mm -0.05 mm), relatively flat or largely undulate and commonly wedging laterally; laminar spacing is not constant, ranging from 13 to 18, rarely 9-10 per 5 mm; secondary laminae are lighter and more diffuse; total number of primary and secondary laminae is generally 18-20 (up to 26) per 5 mm. Thin pillars (0.035-0.045 mm thick), restricted to a single interlaminar space, are simple, spaced up to 7-8 per mm, but more commonly irregularly branching, forming an irregular network. Astrorhizal canals are present but not very numerous, with axial canals from 0.30 to 0.50 mm across. In tangential section (Fig. 11B) pillars appear as round dots but also irregular and joined together to form a cateniform network.

*Remarks:* Specimens typically correspond to the diagnosis of *Intexodictyon* Yavorskii, as given by Stearn et al. (1999). They resemble the Silurian species *I. barlykiense* Yavorskii, 1963 in structural elements, but differ in the presence of astrorhizae. Stock (1991) established the species *I. manliusense* from the Early Devonian (Lochkovian) of New York on the basis of a strong development of two successive growth phases. In the Cantabrian specimens some difference in skeletal growth is observed but this is not rhythmic and is possibly environmental. Specimens are very similar to *Intexodictyon perplexum* by Yavorskii (1963) from the Late Silurian of the Magadan region (Russia), with the same general features and density and development of skeletal elements. The Spanish specimens have slightly smaller astrorhizal canals, but this difference is considered to fall within species variability.

**FAMILY Actinostromatidae Nicholson, 1886**
**GENUS *Plectostroma* Nestor, 1964**
***Plectostroma salairicum* (Yavorskii, 1930)** (Fig. 11C, D)

*Material:* Nieva Fm., Santa María del Mar section, 4 specimens (DPO 39498-39501); Lebanza Fm., Vañes quarry section, 5 specimens (DPO 39502-39506); Lebanza Fm., Lebanza quarry section, 1 specimen (DPO 39507) and Lebanza Fm., Araúz section, 1 specimen (DPO 39508).

*External features:* Most of the skeletons are laminar, up to 4 cm thick and 16 cm in diameter. A few are bulbous, with a diameter of up to 20 cm; some bear small mamelons.

*Internal features:* In longitudinal section (Fig. 11C), skeletal tissue of compact microstructure is dominated by continuous and long pillars with colliculate laminae. In some specimens, a crescentic growth basal layer is developed, with thicker and more irregularly distributed elements defining a latilamination 5 to 10 mm thick. Pillars are generally continuous, locally up to 3-4 mm, and thicker (up to 0.06 mm thick) than colliculi, especially at the basal growth phases; 24 to 28 pillars per 5mm, but in places thinner (0.03 mm-0.04 mm) and more numerous, ranging from 32 to 39 per 5mm. Colliculi, about 0.03 mm thick and from 20 to 25 per 5 mm (locally up to 6-7 per mm), are commonly arched, but also straight, and may arise at uniform levels forming part of a laterally continuous tissue, or at different levels forming an irregular network. Rare dissepiments occur. Narrow and vertically continuous astrorhizae (up to 0.30-0.36 mm diameter) are prominent, with a few lateral canals. In tangential section (Fig. 11D), pillars like solid dots, locally joined by colliculi, produce an imperfect hexactinellid network; astrorhizal canals with axial (up to 0.36 mm) and lateral (0.18-0.21 mm) canals.

*Remarks:* The Cantabrian specimens show the characteristic long and thin pillars and poorly aligned colliculi of *Plectostroma* Nestor, 1964. In comparison with the type species, *P. intertextum* (Nicholson, 1886), these specimens have a lower density of colliculi and a larger astrorhizal diameter.

The specimens also resemble the Chinese species *P. beiliuense* Yang and Dong, 1979, but differ in having more numerous and not so regularly aligned colliculi. The Spanish material is comparable to *P. salairicum* (Yavorskii, 1930) in density and thickness of skeletal elements, the astrorhizae and in alignment of the horizontal colliculi.

**FAMILY Coenostromatidae Waagen & Wentzel, 1887**
**GENUS *Habrostroma* Fagerstrom, 1982**
***Habrostroma centrotum* (Girty, 1895)** (Fig. 11 E, F)

*Material:* Nieva Fm., Santa María del Mar section, 6 specimens (DPO 33544-33549) and Lebanza Fm., Araúz section, 1 specimen (DPO 33550).

*External features:* Skeletons are usually irregularly bulbous, up to 8–10 cm in diameter; but a few are laminar and slightly ragged. Latilamination irregularly developed.

*Internal features:* Latilamination marked by variations in thickness and number of coenostromes and microlamina proximity. Skeletal structure is not uniform: in longitudinal

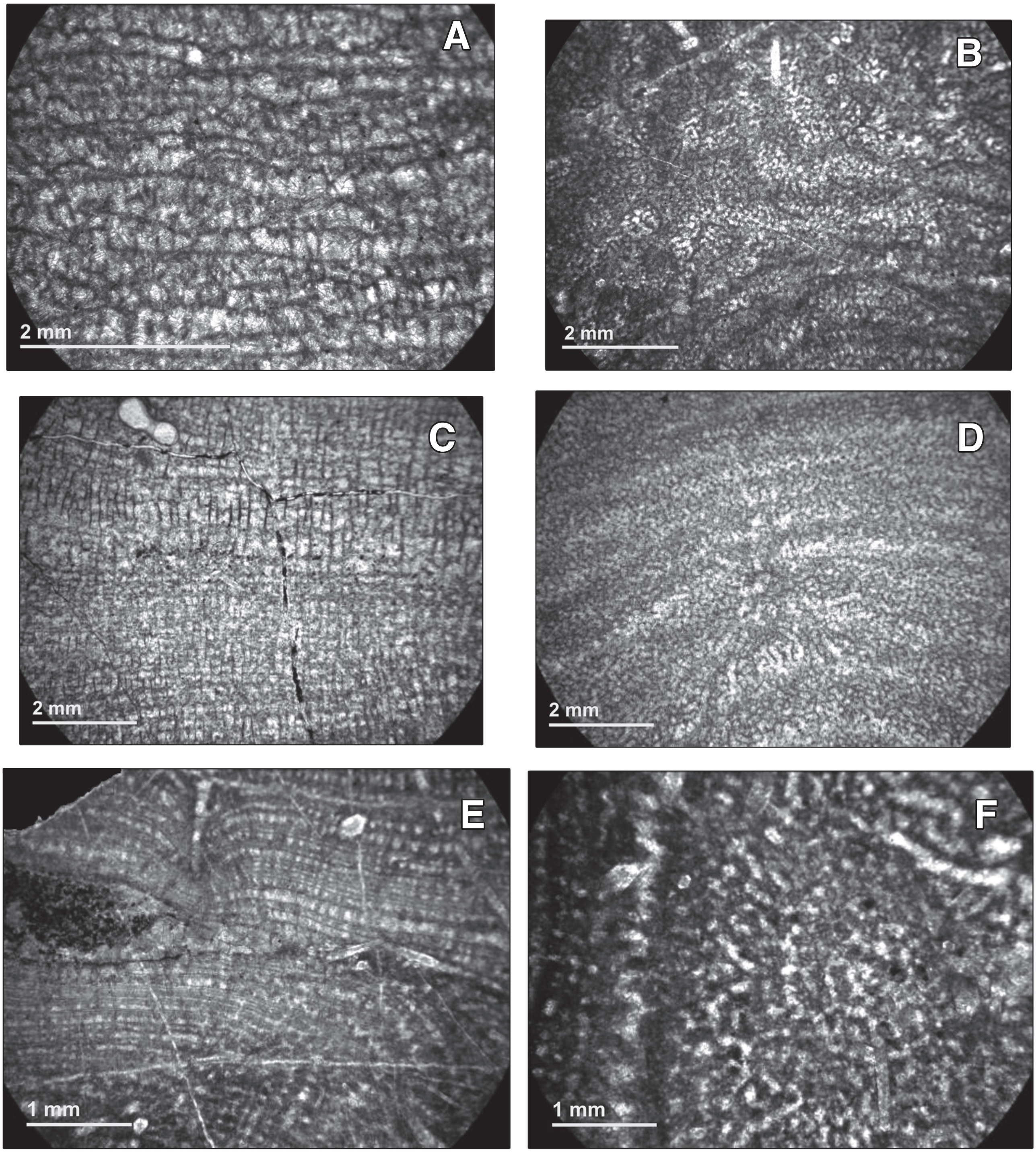


FIGURE 11 | **A-B)** ***Intexodictyon perplexum*** **Yavorskii. A) Longitudinal section. Specimen DPO 33552 from the Santa María del Mar section (Nieva Fm.). B) Tangential section of the same specimen C-D)** ***Plectostroma salairicum*** **(Yavorskii). C) Longitudinal section. Specimen DPO 39498 from the Santa María del Mar section (Nieva Fm.). D) Tangential section of the same specimen. E-F)** ***Habrostroma centrotum*** **(Girty). E) Longitudinal section. Specimen DPO 33547 from the Santa María del Mar section (Nieva Fm.). F) Tangential section. Specimen DPO 33548 from the Santa María del Mar section (Nieva Fm.).**

section (Fig. 11E), coenosteles are the most prominent elements, spaced 23–25 per 5 mm and 0.12 mm thick, but in some instances at tops of latilaminae, coenostromes dominate, locally wrinkled, variably spaced, averaging 16–20 per 5 mm (ranging 10 to 50 per 5 mm), and 0.06 to 0.12 mm thick, containing microlaminae (1 to 4-5) mainly at tops of coenostromes. Microlaminae are wrinkled or cystlike structures, 0.015-0.030 mm thick, spacing variable (from 8–16 per mm to 3–7 per mm); dissepiments not abundant, locally as cyst-like microlaminae. Astrorhizae are commonly numerous, superposed, spaced 4 or 5 mm, with narrow axial canals (<0.30 mm diameter), crossed by dissepiments. Cellular to microreticulate, or locally melanospheric and akosmoreticulate tissue. In tangential section (Fig. 11F), round to anastomotic sections of coenosteles (0.09-0.15 mm across).

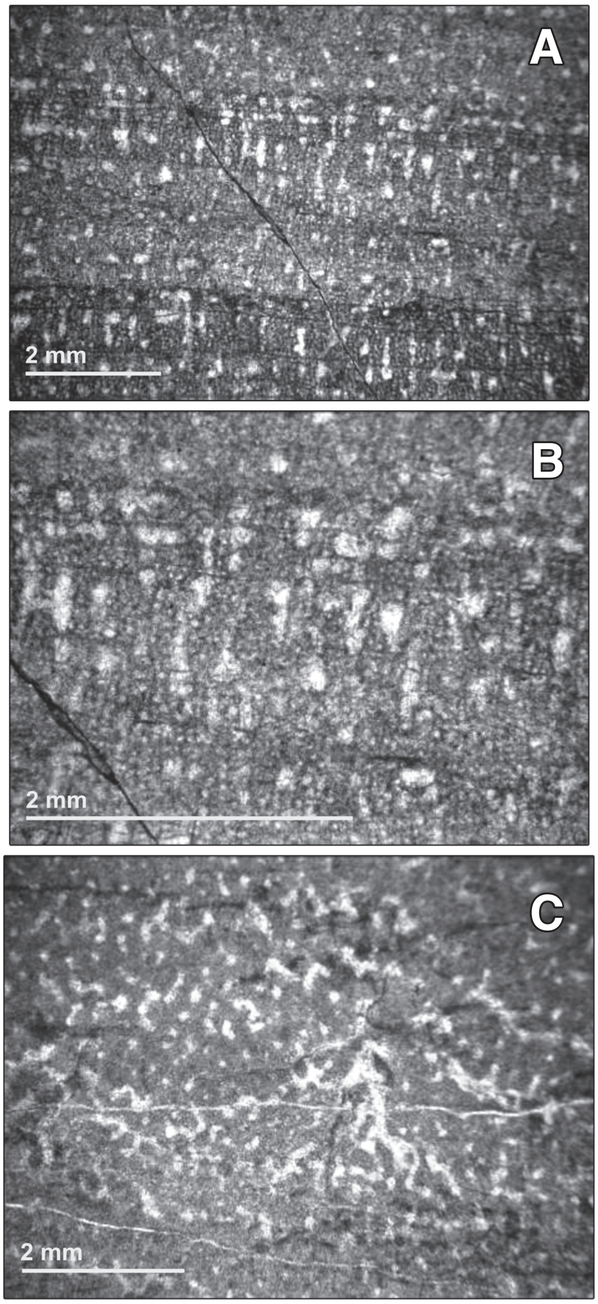


FIGURE 12 | ***Parallelostroma foveolatum*** **(Girty). A) Longitudinal section. Specimen DPO 33561 from the Vañes quarry section (Lebanza Fm.). B) Longitudinal section of the same specimen, detail of microstructure. C) Tangential section. Specimen DPO 33562 from the same locality.**

*Remarks:* The Cantabrian specimens exhibit wide variation within the same thin section, with either coenostromes or coenosteles dominating, agreeing with Stock's definition of *Habrostroma* (see Stock, 1988, 1991). Specimens are similar to *H. centrotum* (Girty, 1895) by their rare cystlike microlaminae, locally superposed coenosteles, and similar density of skeletal elements, although locally they show more prominent coenosteles. They differ from the type species, *H. proxilaminata* (Fagerstrom, 1961), by regular and partly superposed coenosteles, and more irregular coenostromes.

**GENUS *Parallelostroma* Nestor, 1966**
***Parallelostroma foveolatum* (Girty, 1895)** (Fig. 12)

*Material:* Lebanza Fm., Vañes quarry section, 4 specimens (DPO 33561-33564) and Lebanza quarry section, 13 specimens (DPO 33565-39497).

*External features:* Skeletons irregular, up to 40 cm diameter, to domical, up to 34 cm diameter and 25 cm high. Some possess mamelons, 5-7 mm centre-to-centre and 1-2 mm high. Latilamination not well developed, and irregular in thickness, from 1-4 mm.

*Internal features:* In longitudinal section (Fig. 12A, B), weak latilamination marked by difference in thickness of macrostructural elements and number of microlaminae. Commonly thick coenostromes (0.09-0.30 mm), spaced 11 to 20 per 5 mm, but when latilamination is distinct, thinner (0.03-0.06 mm) and closely spaced, 22 to 40 per 5 mm. Coenostromes composed of several microlaminae, commonly 3-4; microlaminae show wide variation in spacing, closely spaced (7-14 per mm) or widely spaced (2-4 per mm). Coenosteles, spaced 13 to 25 per 5 mm, variable in thickness (0.06 to 0.24 mm), and irregular, spool shaped, with parallel sides, confined to an intercoenostrome space, but usually superposed and separated by coenotubes 0.06 to 0.09 mm in diameter. Galleries rounded or irregular, 0.06 to 0.18 mm high. Coenostromes and coenosteles constituted of microreticulate (orthoreticulate) microstructure, very well defined within coenosteles, only locally clinoreticulate. In tangential section (Fig. 12C), coenosteles anastomotic, or irregularly rounded (0.12-0.24 mm thick) and 0.15 to 0.32 mm apart, locally showing a closed network. Small astrorhizae containing axial canals (0.12-0.20 mm across); branching horizontal canals may occur.

*Remarks:* The genus *Parallelostroma* is very similar to *Habrostroma*. According to Fagerstrom (1982) and Stock (1991), the coenostromes in *Parallelostroma* are relatively thicker than those in *Habrostroma* when gallery height is compared, and *Parallelostroma* has orthoreticulate microstructure, whereas in *Habrostroma* this is akosmoreticulate. The specimens described here are strikingly similar to *Parallelostroma foveolatum* (Girty, 1895) from the Early Devonian of New York, redescribed by Stock (1988, 1997). Features fall within the range of skeletal dimensions provided by Stock, although pillar spacing is slightly greater in Cantabrian specimens.

## FAUNAL ASSOCIATIONS

Three types of faunal associations have been observed, hereafter named associations 1, 2 and 3 (Table 1). These three faunal associations occur at specific locations within the framework of the high-frequency deepening upward cycles described above.

### Association 1

Association 1 has been recorded in the Lebanza quarry and Vañes quarry localities. It occurs at the top of thick pack- to grainstone packages that stack vertically without intervening finer-grained lime-wackestone or marlstone/shale intervals, forming top-missing cycles, although the skeletons are embedded in a dark pack- to wackestone, significantly richer in mud than the underlying deposit. Association 1 consists of massive skeletons of stromatoporoids and tabulate corals with rare branching coralla (see Table 1). Encrusting bryozoans are also common. Skeletons are mainly in situ, although some of them are slightly displaced and/or overturned. On sufficiently large bedding surfaces, skeletons of this association appear isolated (Fig. 4C, D) or forming small clusters. These skeletons are small to medium in size (4-20 cm, exceptionally up to 40 cm), possess smooth bases and display irregular or low- to high-domical morphologies. Some skeletons of stromatoporoids and *Squameofavosites* display ragged margins. Also, *Favosites intricatus* and *Squameofavosites* ex gr. *cechicus* typically develop internal banding suggestive of a life span of 3-6 annual cycles (Young and Kershaw, 2005; Berkowski and Belka, 2008). A large quantity tabulate coral shows a skeletal thickening of the most external parts of the coralla. Postmortem overgrowths by small-sized encrusting cystoporate bryozoans are common in the skeletons of this association. Some massive skeletons show both embedment (bioclaustrations) and boring (bioerosion) structures (Tapanila, 2005). Finally, skeletons display a thin coating of microbial micrite and their outer intraskeletal voids are partially or totally filled with peloidal micrite (Bathurst, 1975) (Fig. 10E).

TABLE 1 | **Occurrence of coral and stromatoporoid taxa in the three faunal associations described in this paper. The species *Labechiella* sp. 1 occurs in a rudstone level and therefore it is not assigned to any association.**

**Ocurrence of taxa in the faunal associations**

| Taxa/ Association | Association 1 | Association 2 | Association 3 |
|---|---|---|---|
| *Zelolasma* sp. 1 | absent | abundant | absent |
| *Embolophyllum* sp. 1 | absent | rare | absent |
| *Tryplasma aequabile* | absent | rare | absent |
| *Favosites intricatus* | common | rare | absent |
| *Favosites* aff. *goldfussi* forma *pyriformis* | rare | abundant | common |
| *Squameofavosites* ex. gr. *cechicus* | abundant | rare | absent |
| *Thamnopora yavorskyi* | rare | abundant | rare |
| *Heliolites* cf. *praeporosus* | common | common | rare |
| *Labechiella* sp. 1 | absent | absent | absent |
| *Labechiella* sp. 2 | common | rare | absent |
| *Intexodictyon perplexum* | absent | rare | absent |
| *Plectostroma salairicum* | abundant | rare | absent |
| *Habrostroma centrotum* | absent | rare | absent |
| *Parallelostroma foveolatum* | abundant | common | absent |

### Association 2

Association 2 has been recorded in the Santa María del Mar, Lebanza quarry and Vañes quarry localities. It is present at the top of thin pack- to grainstone packages, below a marlstone/shale interval, or in the overlying argillaceous wacke- to packstones.

This association consists of branching colonies of phaceloid rugose (*Zelolasma* sp. 1) and tabulate (*Thamnopora yavorskyi*) corals with small globose favositids (*Favosites* aff. *goldfussi* forma *pyriformis*). Stromatoporoids and other tabulate corals also occur (Table 1). Finally, scarce auloporids, fenestrate bryozoans, solitary rugose corals and brachiopods are also present. Where exposed on large bedding surfaces, the second association consists of isolated skeletons (Fig. 4A, B) although some branching rugose corals form small (ca 1 m in diameter) biostromes. Massive coralla are mostly small (5-10 cm in diameter) and spherical or low-domical. Stromatoporoids are, in general, smaller than in association 1 and display either low-domical to irregular or, subordinately, laminar encrusting morphologies. Massive corals and stromatoporoids usually possess smooth bases and growth-interruption surfaces. In contrast to association 1, seasonal growth bands are only shown by some skeletons of *Favosites intricatus*, pointing to a very short life span (1-2 annual cycles) (Young and Kershaw, 2005;

Berkowski and Belka, 2008). Colonies assigned to *Favosites* aff. *goldfussi* forma *pyriformis* commonly show a growth form highly dependent on the environment. Most of them display a radial, sometimes circumrotatory, pattern, with usual episodes of regeneration following partial mortality or movements.

In this association, post-mortem and live overgrowths made by encrusting cystoporate bryozoans, auloporids and stromatoporoids are very common, with bryozoans reaching a greater skeletal development than in association 1. Nevertheless, both bioperforations and bioclaustrations are rare. Thin microbial crusts are present on skeletons, as in association 1.

### Association 3

The third association has only been detected in the Lebanza quarry section, being generally found in the marlstones and shales of the upper part of the cycles. It mainly consists of scattered, tiny (about 1-2 cm in diameter), globose to hemispherical favositids (*Favosites* aff. *goldfussi* forma *pyriformis*), which show a radial or hemispherical pattern of growth, and rare branching tabulates (*Thamnopora yavorskyi*). In addition, small brachiopods assigned to *Howellella corallina* are abundant.

Noticeably, overgrowths, bioperforations and bioclaustrations are absent. No data exist about the presence of microbial crusts on skeletons.

## DISCUSSION

### Palaeoenvironmental interpretation

The Nieva and Lebanza formations belong to distant sectors of the sedimentary basin. If a palinspastic restoration were applied by roughly displacing the allocthonous units towards the inner parts of the orogen (Fig. 1), the Nieva section would be located west of its present day location, whereas the Lebanza quarry sections in the Palentine nappes would shift to the south, to a point which is presently somewhere below the Tertiary cover of the Duero Basin. Despite lying more than one hundred kilometres apart along strike, they show similarities in terms of facies and vertical stacking as well as in faunal associations.

Facies analysis and the widespread occurrence of HCS beds suggest that the deposits of both formations were laid down on a storm-dominated ramp. Facies range from inner ramp cross-bedded limestones, deposited above fair-weather wave base, to middle ramp HCS grainstones and marlstone alternations, and finally to middle-to-distal ramp argillaceous wacke- to packstones, marlstones and shales. In addition, some intervals of argillaceous wacke- to packstones, marlstones and shales, must have been deposited on a protected shelf. Finally, peritidal peloidal limestones and mudstones account for the shallowest reaches of the depositional system. In the case of the best exposed Lebanza Fm. (Fig. 3C; see also Krans et al., 1980), the vertical passage from Member A to Member B is thought to record an overall shallowing upward trend ending with shoreface conditions where high angle cross-bedded deposits prevailed. The overlying deposits of Member C, with common signs of microbial activity and containing the in-situ reefal fauna, would largely represent a protected environment, finally evolving into the peritidal deposits of Member D. These would record a maximum regressive episode before shelfal conditions were re-established in Member E. At large scale, in the Lebanza Fm., the presence of in situ reefal fauna in Member C suggests that reef growth could be related to the establishment of lower energy conditions than those represented by the cross-bedded limestones of Member B. It remains unclear whether the protected shelf was created behind a shoreface bar complex (Member B) through a large scale progradation (see Krans et al., 1980) or it was due to regional scale tectonism resulting in the individualization of sills and intervening protected areas. It has been claimed that this structural imprint explains the facies distribution of some Devonian units (e.g. Keller, 1997; Hofmann and Keller, 2006), although there is no agreement over the significance, location and present-day identification of those faults and palaeohighs (see comments in Fernández et al., 2006).

Superimposed on this large scale trend, the overall arrangement of fining upwards cycles from grain-supported detrital limestones to marlstones or shales is interpreted to represent high frequency deepening upward cycles, each reflecting a base-level fall followed by a base-level rise. In this context and judging from their location within cycles, reefal deposits began forming once a relative base level rise had taken the sandy sea-bottom, represented by the grain-supported detrital limestones, to deeper or sheltered conditions where it was not as frequently affected by the mostly storm-related currents. This situation has been interpreted as having taken place in other small Devonian build-ups of the Cantabrian Zone (e.g. Fernández et al., 2006).

### Association 1

The mode of occurrence of this association, on top of thick limestone packages, which amalgamate without finer-grained caps, suggests that it is the shallowest association. This is in agreement with the types of corals and stromatoporoids present, which point to a well-aerated environment with high light levels (corallum morphology, internal banding, growth rate…). Nevertheless, judging also by the encasing mud-rich sediment, energy levels must have been moderate. The occurrence of skeletons on top of the limestone packages indicates that these organisms colonized a relic granular sea bottom once the currents that had accumulated the skeletal sediments were no longer active; their dominant domical morphology also points to a suprastratal growth (Wood, 1999) not coeval with an intermittent sediment input. In this sense, the presence of ragged margins in some stromatoporoid and *Squameofavosites* skeletons, traditionally interpreted as having been formed by episodic sedimentation (Kershaw and Riding, 1978; Miller and West, 1997), is here considered rather as being due to other causes (for instance, the formation of primary cavities in the early stages of skeletal growth, as proposed by Kershaw et al., 2006). These time relationships between reefal organisms and their substratum have also been deduced for other Devonian deposits of the Cantabrian Zone (cf. Fernández et al., 2006). The skeletal thickening of the most external parts of the coralla could represent a reaction to stress, possibly related to the cause of death. The microbial biofilm postdates the death of reefal organisms and we hypothesize that increased microbial activity resulting in biofilms could be related to the same processes that caused their death. It is possible that a process leading to nutrification could have provoked the decline of skeletons and the development of microbial crusts. In this sense, MacNeil and Jones (2008) associate the nutrification processes with sea level oscillations.

## Association 2

The mode of occurrence of this association, on top of thinner skeletal limestone packages or in the overlying argillaceous wacke- to packstones, as well as the branching morphology of skeletons, suggest a lower energy level (cf. also Stevens, 2008) than in the previous case. A well aerated environment, but with moderate light penetration, is invoked for this association, which, in contrast to association 1, shows evidence of significant sedimentation taking place during skeleton growth. The phaceloid morphology of *Zelolasma* colonies suggests a constratal growth without a substantial projection above the substrate (Wood, 1999). Growth-interruption surfaces of massive corals and stromatoporoids (Kershaw et al., 2006) and rapid growth rate of corals, suggested by offsets in *Favosites* aff. *goldfussi* forma *pyriformis*, point to episodic sedimentation. This species seems to have been adapted to live on, and partially buried in, soft-bottom substrates, usually between major episodes of terrigenous-mud influx (e.g. Gibson and Broadhead, 1989).

## Association 3

This association would reflect the colonization of a muddy bottom in a deeper and/or more sheltered area by scattered, stunted favositid colonies. The small size and the globose morphology of colonies would probably be related to high rates of terrigenous mud sedimentation.

## Palaeobiogeographic remarks

Lochkovian-Pragian reefs are rare and less well-known than their Silurian or later Devonian counterparts, and the majority developed in Laurentia and the Urals (Copper, 2002; Antoshkina and Königshof, 2008). Gondwanan Pragian reefs are known from Bohemia (Koněprusy Limestone), France (Armorican Massif), Spain (Cantabrian Mountains, Ossa-Morena Region), Saudi Arabia (Al Jawf) and Pakistan (Nowshera) (Chlupáč, 1967; Pelhate and Plusquellec, 1980; Copper, 2002; Rodríguez et al., in press), but only those from Bohemia and France have been studied in detail.

A comparison between the deposits described in this paper and other Pragian reefs is difficult because of the different reefal settings recorded in each region. Nevertheless, the paucity, or even absence, of algal and microbial communities as frame builders is remarkable when compared to deposits from elsewhere, e.g. Australia (Adachi and Ezaki, 2007) or the Urals (Antoshkina and Königshof, 2008). There are no data currently available to explain these differences. Nevertheless, it is worth noting that even though they are extremely rare, microbial sediments do appear together with the reefal fauna in Member C of the Lebanza Fm. and in the studied deposits of the Nieva Fm. This could indicate a complex relationship between metazoan and microbial communities. They appear together and, as mentioned above, microbial crusts seem to be related to the death of metazoans (cf. Montaggioni and Braithwaite, 2009). However, this is beyond the scope of this paper and will require further work.

Nevertheless, a faunal comparison can be carried out in order to shed light on the palaeobiogeographic relationships during Pragian times.

The rugose coral genera of these sections were largely widespread during the Early Devonian. *Tryplasma* was cosmopolitan, *Embolophyllum* is known in the NE of Russia (Kolimia and Taimyr), Australia (Victoria, New South Wales and Queensland) and China (Qinghai, Xizang and Sichuan) and *Zelolasma* is also known in Tadzhikistan (N Afghanistan), Australia (New South Wales) and NE Rusia (Taimyr) (Hill, 1981).

The genera of tabulate corals described above are cosmopolitan, especially from the Emsian onwards (Birenheide, 1985). At the species level, these faunas show close affinities with the Bohemian tabulate corals and thus, three of the species recorded here were first described from the Koneprusy Limestone (*Favosites intricatus*, *Squameofavosites cechicus* and *Heliolites praeporosus*). The favositid species have been cited in several outcrops from the Urals and other former Soviet regions, where *S. cechicus* has been assigned to *Favosites bohemicus* (Počta). In addition, *Thamnopora yavorskyi* is a species from the Early Devonian of the Kuznetsk Basin. For specific references in the literature to species distribution, see the remarks section in the chapter "systematic palaeontology".

The stromatoporoid fauna is peculiar and is represented by a mixture of widespread forms typical of the Silurian (*Plectostroma*, *Intexodictyon*, *Parallelostroma*) and by other genera possibly derived from the earliest Devonian faunas of North America (e.g. *Habrostroma*) (Stearn et al., 1999). Apart from these genera, *Labechiella* was very rare in the Early Devonian and up to now it was only known in the Late Lochkovian in Australia (Queensland) (Fernández-Martínez et al., 2008).

## CONCLUSIONS

The Nieva and Lebanza formations belong to sectors of a sedimentary basin that were originally more than one hundred kilometres apart along strike. Despite this, they show similarities in terms of facies, vertical stacking and fossil assemblages. Facies analysis suggests deposition in a storm-dominated ramp, ranging from shoreface cross-bedded limestones, to middle ramp deposits with HCS, and to middle to distal ramp argillaceous wacke- to packstones, marlstones and shales. Protected shelf deposits, depicted by some intervals of argillaceous wacke- to packstones, marlstones and shales, and peritidal peloidal limestones and mudstones complete the range of facies. Those deposits are mainly arranged into high frequency fining and deepening upward cycles.

In the studied interval, three fossil assemblages are described, which are interpreted to correspond to relatively distal or protected settings. These three associations take place in specific positions within the context of high frequency cyclicity. This mode of occurrence of reefal deposits suggests that they began forming once a relative base level rise had taken a sandy sea-bottom, represented by the grain- to packstone skeletal limestones, to deeper or sheltered conditions, where it was not as frequently affected by storm-related currents. The first reef association, with massive colonies, suggests deposition in higher-energy, shallower areas than the second association, mainly characterised by branching colonies. Finally, the third association would reflect the colonization of a muddy bottom in a deep or sheltered ramp setting by scattered, stunted favositid colonies and by small brachiopods.

Palaeobiogeographically, the coral genera were widespread during the Early Devonian, the species of tabulate corals showing close affinities with those from Bohemia and, to a lesser extent, from the Urals. The stromatoporoid fauna displays both Silurian and Early Devonian affinities.

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