Rivista Italiana di Paleontologia e Stratigrafia	volume 113	no. 3	5 pls.	pp. 307-328	December 2007

DEVONIAN TABULATE CORALS, CALCAREOUS ALGAE, AND BIOCLAUSTRATIONS FROM THE KARAKORUM MOUNTAINS (NORTHERN PAKISTAN)

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Received: March 12, 2007; accepted: August 4, 2007

Key words: Devonian, Tabulata, Algae, Bioclaustrations, Karakorum, Pakistan.

Abstract. During several field work campaigns to the Karakorum Mountains samples containing Devonian macrofossils were collected by M. Gaetani and P. Le Fort, mostly in the uppermost Yarkhun Valley (Northern Pakistan). Generally, Devonian rocks are outcropping rather extensively in several thrust sheets of the Northern Karakorum Terrain, namely in the Chillinji, Baroghil/Lashkargaz, and the Karambar Units. The dolostones of the Tash Kupruk Zone, similar to the Chilmarabad Fm. of the previous units, are also Devonian in age. Fossils mentioned below originate from measured logs (Yarkhun River, Chillinji, Ribat), others from isolated localities.

Identification of most of the fossils on species, or even at genus-level is difficult due to their moderate to poor state of preservation. Recrystallisation phenomena that had affected particularly porous skeletons, especially those with small-sized intra-skeletal cavities (i.e. intra-tabular spaces of small-sized tabulate corallites, and inter-laminar spaces of stromatoporoid skeletons) often preclude reliable determination. Nevertheless, from the following formations tabulate corals and calcareous green-algae could be determined: Chilmarabad Fm. (Lashkargaz/Baroghil Unit), Shogram Fm. (Yarkhun River section), Margach Fm. (Ribat section), the Tash Kupruk dolostones (loose blocks north of Inkip).

The taxa described are *Pseudopalaeoporella* ? sp., *Receptaculites* cf. *chardini*, *Pachyfavosites polymorphus*, *Thamnopora grandis*, *Thamnopora* cf. *longdongshuiensis*, *Thamnopora* cf. *reticulata*, *Celechopora devonica*, *Alveolites (Alveolites) hudlestoni*, *Heliolites*? sp., *Pachycanalicula*? sp., "*Caunopora*", and *Helicosalpix asturiana*.

Most of the fossils described point to Middle to Upper Givetian age, although they are not particularly age diagnostic.

Riassunto. Campioni contenenti macrofossili devoniani sono stati raccolti durante diverse spedizioni in Karakorum da M. Gaetani e P. Le Fort, principalmente nell'alta valle di Yarkhun (Pakistan settentrionale). Le rocce devoniane affiorano in modo relativamente esteso in diverse unità tettoniche del blocco del Karakorum settentrionale, in particolare nei thrust sheet di Chillinji, Baroghil/Lashkargaz e Karambar. Le dolomie della Zona Tash Kupruk, simili alla Fm. Chilmarabad delle precedenti unità strutturali, sono pure di età devoniana. I fossili studiati provengono o da sezioni misurate (Yarkhun River, Chillinji, Ribat), oppure da località isolate.

Il riconoscimento di molti dei campioni a livello specifico o addirittura a livello generico è reso difficile dallo stato di conservazione mediocre o scarso. La ricristallizzazione, che ha interessato in modo particolare le strutture scheletriche porose specialmente quelle con cavità intrascheletriche di piccole dimensioni (come gli spazi intratabulari dei coralliti tabulati di piccole dimensioni e gli spazi interlaminari degli stromatoporoidi) spesso impedisce una determinazione affidabile. Ciò nonostante sono stati identificati coralli tabulati e alghe calcaree bluverdi nelle Fm. Chilmarabad (Lashkargaz/Baroghil thrust sheet), Fm. Shogram (sezione Yarkhun River), Margach Fm. (sezione Ribat), dolomite della Zona Tash Kupruk (Inkip/Lasht).

Le forme descritte sono: *Pseudopalaeoporella*? sp., *Receptaculites* cf. *chardini*, *Pachyfavosites polymorphus*, *Thamnopora grandis*, *Thamnopora* cf. *longdongshuiensis*, *Thamnopora* cf. *reticulata*, *Celechopora devonica*, *Alveolites (Alveolites) hudlestoni*, *Heliolites* ? sp., *Pachycanalicula* ? sp., "*Caunopora*", and *Helicosalpix asturiana*.

La maggior parte dei fossili descritti suggerisce un'età Givetiana, media o superiore, sebbene essi non siano particolarmente diagnostici per l'età.

Introduction

This paper deals with tabulate corals, calcareous green algae, and bioclaustrations collected in the uppermost Yarkhun Valley during several field work campaigns (1992, 1996, 1999, 2004). Some of them were collected by P. Le Fort in 1992, all the other samples were obtained by M. Gaetani. This paper is the companion of the Schroeder's paper (2004) on the Devonian rugose corals.

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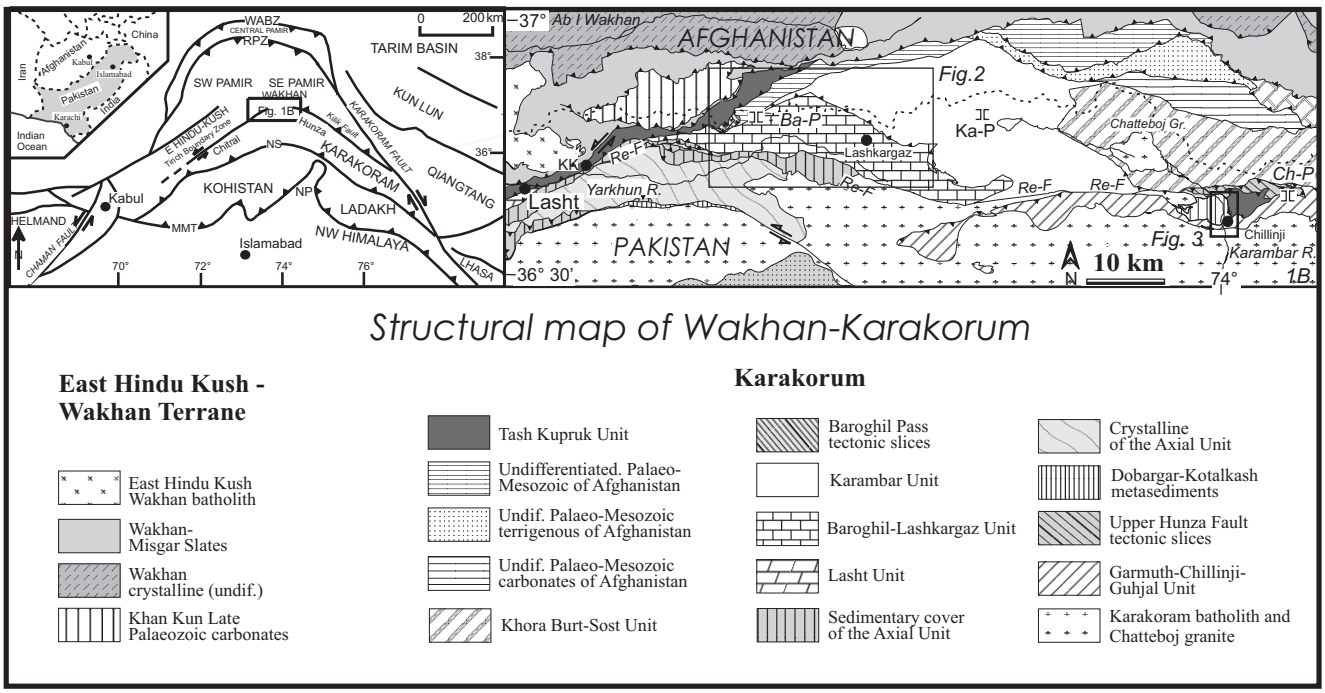


Fig. 1 - Index map of the Western Karakorum and Eastern Hindu Kush.
Acronyms: KK = Khan Kun; Ba-P = Baroghil Pass; Re-F = Reshun Fault; Ka-P = Karambar Pass, Ch-P = Chillinji Pass; dotted line = Pakistan-Afghanistan border.

This is the first description of such a kind of fossils in the area. A general discussion of the stratigraphy may be found in Gaetani (1997), whilst further details on the Devonian stratigraphy may be obtained in Talent et al. (1999) and in Gaetani et al. (submitted).

Geological setting

The North Karakorum Terrain, as defined in recent papers (Zanchi & Gaetani 1994; Gaetani et al. 1996; Zanchi et al. 2000) consists of a thick and polyphase stack of thrust sheets which lay north of the Karakorum Batholiths (Le Fort & Gaetani 1998) (Fig. 1). In the Chitral region, the Karakorum is separated from the East Hindu Kush - Wakhan by the Tirich Boundary Zone, a left lateral shear zone including deformed ultramafic rocks (Zanchi et al. 1998, 2000). East of the Shah Jinali Pass, the Tirich Boundary Zone is tectonically elided by NE-SW left-lateral strike-slip faults and the Palaeozoic Wakhan and Misgar slates of Wakhan are directly stacked against the Karakorum units.

The North Karakorum Terrain includes several thrust sheets showing complex geometrical relationships (Fig. 1, 2). To the northwest, the Tash Kupruk Zone contains alkali basalts, tuffs and dolostones, bounded by shear faults. The dolostones are mildly metamorphosed, and contain Devonian Tabulata (this paper). To the south of the Tash Kupruk, Devonian rocks are present at least in three thrust sheets, named Siru Gol, Lashkargaz/Baroghil, and Karambar (Gaetani et al. 2004). Southwards, a major partition is marked by the Reshun Fault (Pudsey 1985; Zanchi et al. 1998, 2000), which connects to the Upper Hunza Fault in the east, over a distance exceeding 200 km (Fig. 1). South of this fault, tectonic units locally include the pre-Ordovician crystalline basement and Palaeozoic/Mesozoic sediments with reduced thickness. Devonian rocks are mostly absent, but in the Chillinji Unit, where an almost complete Palaeozoic succession unconformably covering pre-Ordovician intrusives is exposed (Fig. 3).

The lithostratigraphic units concerned with this paper are the Chilmarabad, Shogram and Margach formations (Fig. 4). The Chilmarabad Formation consists mainly of light grey dolostones, medium to thick bedded, typically yellowish when altered. In its lower part and in the southernmost thrust sheets the formation is enriched in clastics, from arenites to fine conglomerates, with typical black chert clasts. The upper part frequently contains peritidal cycles with fenestrae and it is mostly devoid of terrigenous input. In the Lashkargaz/Baroghil thrust sheet this part is rather rich in tabulate corals, stromatoporoids, and algae. The topmost beds of the Chilmarabad Fm. may show evidence of supratidal condition with emersion (tepee structures in the Ribat section).

The Chilmarabad Fm. is disconformably overlain by fine conglomerates and sandstones, coarsely bedded, 12 to 30 m thick, forming the base of the Shogram Formation. This terrigenous lithozone is present in all

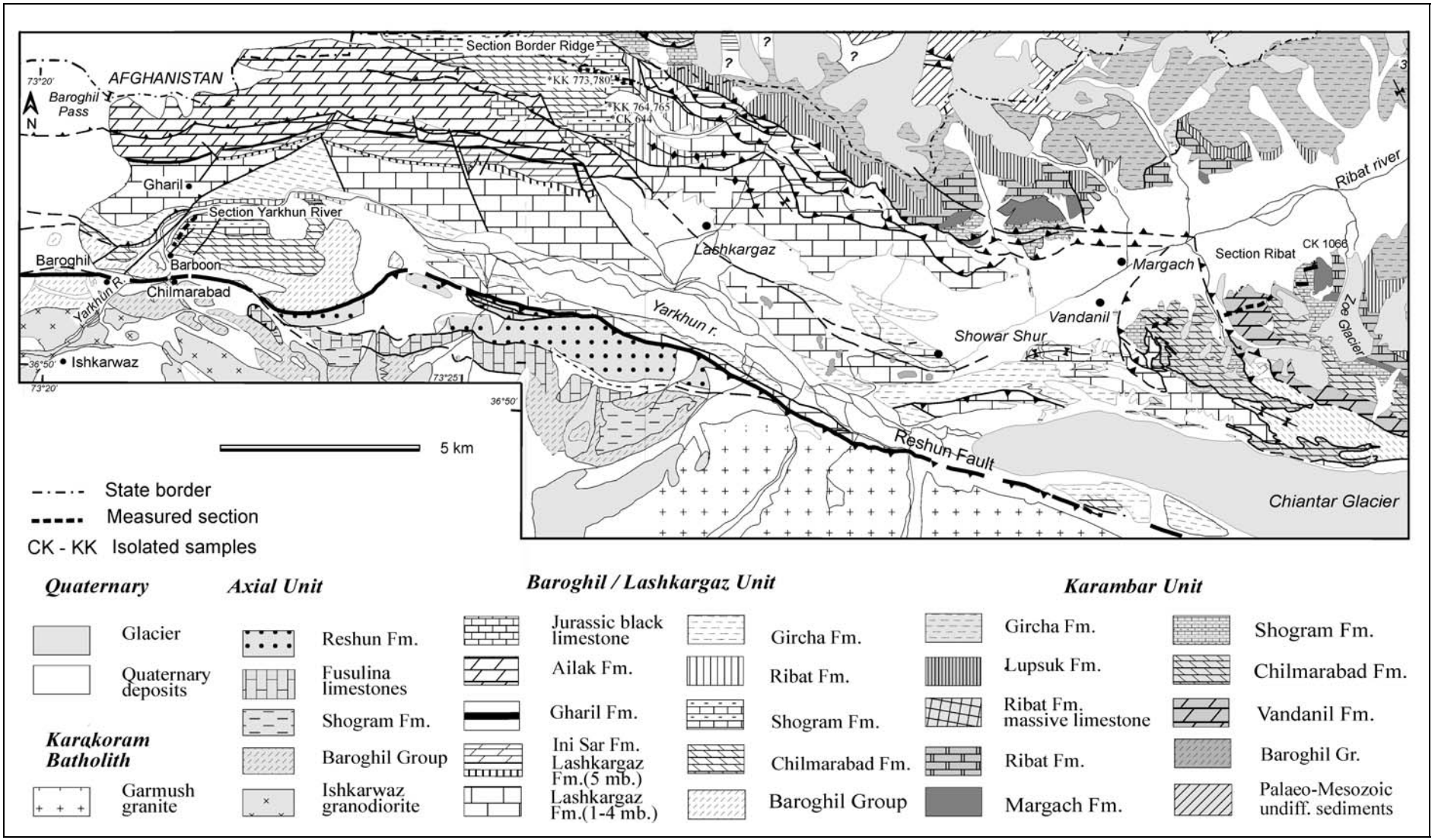


Fig. 2 - Simplified geological map of the Baroghil - Ribat area, with position of the stratigraphic sections and fossiliferous localities. (From Zanchi in Gaetani et al. 2004, modified).

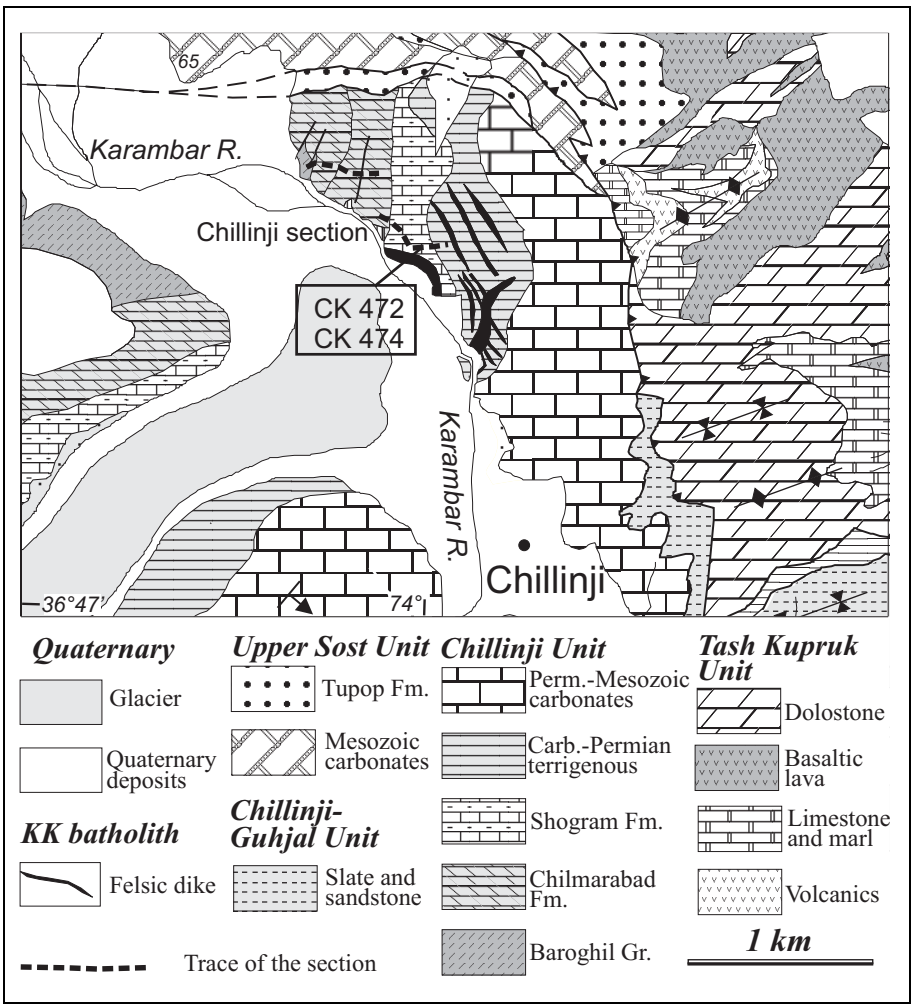


Fig. 3 - Geological map of the Chillinji area, with position of the section Chillinji. (From Zanchi in Gaetani et al. 2004).

the studied outcrops; and locally the microconglomerates contain once again the black chert pebbles. This unit is gradually replaced by alternating fine arenites, siltstones and grey arenaceous limestones in evenly defined beds. In the lower part of the Shogram Fm., a package of about 15-20 m contains abundant brachiopods, as well as tabulates and corals in the Lashkargaz/Baroghil Unit.

The Shogram Fm. develops upwards with alternating grey packstone/wackestones and fine arenites for about 30 to 100 m. This package is capped by one or two coral bafflestones, most typical in the landscape, 10 to 35 m thick.

In the Ribat section, and on the west ridge of the Peak 5391 to the north of the Aksu pass, it was observed a peculiar horizon, less than one m thick, packed with *Receptaculites* cf. *chardini* (sample CK 1066). It lies about 145 m above the top of the coral bafflestone and it is in the lowermost part of the Margach Fm. This unit consists in the lower part of dark grey to dark green splintery siltstones intercalated with thin-bedded arenites, rarely with parallel laminations; rare intercalations of bioclastic limestones bearing brachiopods and crinoid fragments. The whole section is described in Gaetani et al. (2004).

The dolostones of the Task Kupruk are usually mildly metamorphosed. Often, on the altered surface, ooidal grainstone/packstones, heavily recrystallized might be recognized, with fragments of stromatoporoids, algae, rugose and tabulate corals, suggesting the deposition on shoals with rather high energy. Usually the preservation is poor and only to the west of Inkip, is lightly improved.

Summarizing, the described specimens originates from these samples (Fig. 2, 3):

Chilmarabad Fm.

Samples KK 764, KK 765, Lashkargaz/Baroghil Unit, ridge of the dolomitic plateau to the east of the Darvaz An, at an altitude of about 4300 m a.s.l., along the Afghan/Pakistan border. Collection P. Le Fort, 1992.

Shogram Fm.

Sample CK 371, CK 718, Yarkhun River section, lower part.

Sample CK 377, Yarkhun River section, upper bafflestone horizon.

Sample CK 644, lower part of the formation, northwest of Lashkargaz, at 4160 m a.s.l.

Sample KK 773, lower part of the formation, northwest of Lashkargaz, at about 4100 m a.s.l. Collection P. Le Fort, 1992.

Samples CK 472 and some 20 m above CK 474, Chillinji section.

Margach Fm.

Sample CK 1066, Ribat section.

Tash Kupruk dolostones

Sample CK 853 originates from loose blocks at the base of the yellowish rounded dolostone wall that first crops out to the north of Inkip, near Lasht, at about 3400 m a.s.l., on the east side of the Khushrao Gol.

Debris samples

CK 35, loose blocks to the west of Rukut, in front of Lasht, Upper Yarkhun Valley.

CK 500, the tabulate specimen was collected in the scree north of Zhoe Wurt camping ground in the upper Chapursan valley. No Devonian rocks were mapped to the east of the Chillinji An. Since corals have been seen as pebbles in the Gircha Fm. (Lower Permian) elsewhere in the Chapursan valley, it may be that also this sample has the same origin.

Ages

The here described fossils are not particularly age diagnostic. However, as in the case of the Tash Kupruk Zone, they are precious to substantiate and support the lithological correlation of the dolostones to the Chilmarabad Fm. This last unit seems to be bracketed within the middle Devonian, at least in its upper part, but no major precisions are presently possible. In the medium-upper part of the underlying Vandanil Fm. a single sample yielded conodonts of latest Silurian to mid Early Devonian age (R. Mawson, Sydney, pers. comm., 2005).

The Shogram Fm., being more fossiliferous allows finer subdivisions. The lowermost fossil horizon is referred to the Givetian, possibly late Givetian, because of corals (Schroeder 2004). The coral bafflestone is of Frasnian age (Schroeder 2004). The lower part of the Margach Fm. could be still Devonian, but evidence is scanty.

Systematic Palaeontology

Specimens described are stored at the Paleontological Museum of the University of Milan, Italy, under the numbers MPUM 9715 - 9732.

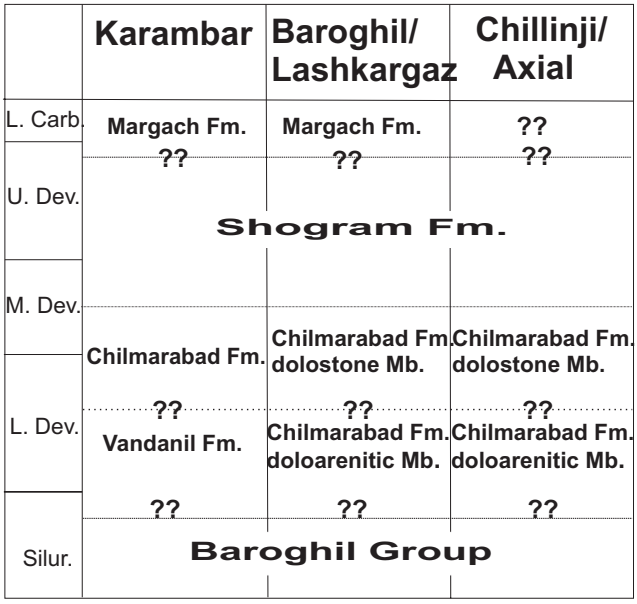


Fig. 4 - The lithostratigraphic subdivisions of the Devonian in Western Karakorum. Time scale according to Gradstein et al. (2004).

Calcareous green algae

Division **Chlorophyta** Papenfuss, 1946

Class **Chlorophyceae** Kützing, 1843

Order **Siphonales** Wille, 1884

Family Halimedaceae Link, 1832

Genus *Pseudopalaeoporella* Mamet & Preat, 1985

Type species: *Palaeoporella lummatonensis* Elliot, 1961, p. 251-254, pl. 9, figs. 1-5, pl. 10, figs. 1-4; from the Middle Devonian of Torquay, Great Britain.

Diagnosis. Plant consists of long cylindrical segments, rounded in cross-sections. Internally, the structure is a typically representative of halimedaceans, being composed of a medullary zone build up by longitudinal filaments turning towards the exterior and branch within the cortical zone. The boundary between medulla and cortex is usually indefinite or irregular (cf. Mamet & Preat 1985).

Pseudopalaeoporella? sp.

Pl. 1, figs 1, 2

Material. Sample KK 764: Three specimens. Thin sections KK764/b1 and KK764/b2. MPUM 9715/1-2. Chilmarabad Fm., Eifelian-Givetian?

Description. Preservation of thalli is rather poor thus restricting a reliable determination. In all sections the thalli show medullary cores consisting of sparitic crystals. The cortical zone is build up by a dark dense pseudomicritic layer. By using Folk's "white-card-method" (Folk 1987) and/or illumination by darkfield condensator, primary structures within the cortical zone, i.e. very thin and densely packed filaments, may be contrasted.

Diameter of thallus about 850 to 1200 µ; medullar zone is usually 350 to 420 µ in diameter.

Remarks. Already Elliot (1961) recognized that internal structures of *Pseudopalaeoporella* are very rare to observe and assumed that during life calcification was poor in the medullar region. This feature seems to be rather characteristic for the genus (Mamet & Preat 1985, Hubmann 1990) together with the very fine cortical filaments which are however sensitive to diagenetic alteration. Since Vachard (1993) assumed a red algal nature because of the very thin cortical filaments and Hubmann & Fenninger (1997) discussed an affiliation to Gymnocodiaceans due to the presence of globular structures in the cortical zone that might be interpreted as reproductive organs, *Pseudopalaeoporella*'s systematic position is unclear.

Geographical and stratigraphical distribution. Currently *Pseudopalaeoporella* is known from the Middle Devonian of the European realm: South-England (Elliott 1961), Belgium (Mamet & Preat 1985, 1987), Germany (Koch-Früchtl & Gee 1994), the Urals (?) (Shuysky 1987), Poland (A. Preat; pers. commun. 1993), Austria (Hubmann 1990; Hubmann & Fenninger 1993), and the Armorican Massif (Vachard 1993).

Order **Receptaculitales** Sushkin, 1962

Family Receptaculitaceae Eichwald, 1860

Genus *Receptaculites* Deshayes, 1828

Type species: *Receptacules neptuni* (Defrance, 1827)

Diagnosis. Usually globular shaped individuals with internal morphology consisting of a central axis and radially arranged branches. On their outer surface branches appear as polygonal (hexagonal or rhomohedral) facets.

Remarks. "Sun-flower shaped inclusions" in Paleozoic rocks generally were long described as sponges or even problematic fossils. Specimens found are usually globular to platter shaped, and measure from some 10 mm to over 30 cm across. The surface is covered by rectangular plates arranged in intersecting sets of clock-wise and anticlock-wise patterns. Since the 70ties of the 20th century several authors (Rietschel 1969, 1970; Nitecki 1970, 1972, etc.) have proposed a green algal assignment because of close morphologic affinities to the plant kingdom rather than animals.

Receptaculites cf. **chardini** Nitecki & Lapparent, 1976

Pl. 1, figs 3-6

Material. Sample CK 1066: One specimen. Thin sections CK1066/1-6 (3 cross-sections, 3 longitudinal sections). MPUM 9716. Margach Fm., Ribat section, Upper Devonian?

Description. Thallus shape globose, slightly flattened to flat up to 10 cm and more. Calcification occurs heaviest apically. Inner wall massive with digitate structures pointing toward interior; digitate structures fingerlike. Laterals (branches, "meromes") stout in adult, thin when immature; inner part of laterals thin, outer part of laterals heavily calcified.

Length (L) of laterals 6.65-6.92 mm (mean 6.80 mm), diameter (D) 2.61-3.29 mm (mean 2.99 mm), ratio of L:D 2.10-2.55 (mean 2.28).

Remarks. The studied receptaculid resembles in general body shape, in the manner of calcification, and in the shape of the lateral *Receptaculites chardini*. It differs from *R. chardini* in dimensions of the laterals which are on average 15 mm (8.7-20 mm) in length and on average 5 mm in diameter. The L:D ratio is comparable to the studied material.

Geographical and stratigraphical distribution. *Receptaculites chardini* was described from the Frasnian of Central Afghanistan.

Tabulate corals

The systematic procedure with tabulate corals is handicapped due to the absence of directly comparable living organisms. Since the biological significance of structural and morphological features of tabulates are not clearly understood till this day, the quality rating of taxonomic characters has been changing through science history. In general differentiation on genus level is mainly based on combined morphologic characters as arrangements of septal elements, wall and pores, formation of tabulae, tabellae and dissepiments, etc. Species discrimination is mainly based on quantifiable, biometric characteristics, e.g. diameter of corallites, thickness of walls, pore-diameter etc.

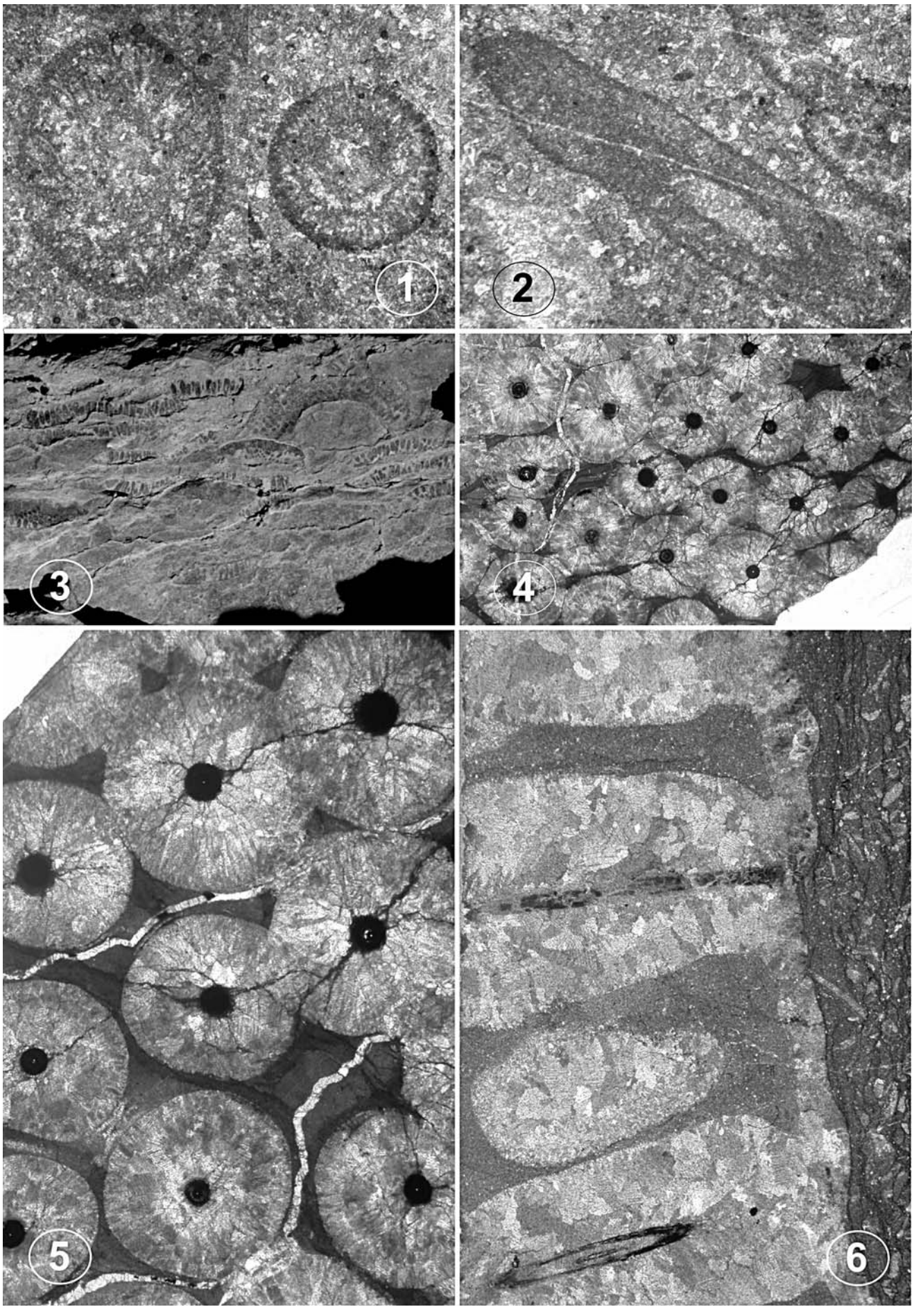
Biometry

Generally, tabulate corals are morphologically simple, and several characters can be quantified by biometric studies. Measurements on 20 corallites per corallum for particular characteristics is calculated to be

PLATE 1

Fig. 1-2 - *Pseudopalaeoporella*? sp.
1: MPUM 9715/2, oblique cross-section showing arrangement of thin, branched cortical filaments. 2: MPUM 9715/1, cross-section of thallus showing non-calcified medullary zone and a cortical rind.

Fig. 3-6 - *Receptaculites* cf. *chardini* Nitecki & Lapparent, 1976.
3: MPUM 9716/4, mass occurrence on weathered surface; 4: densely arranged laterals in cross-section, x 6.5; 5: laterals in cross-section, x 19; 6: MPUM 9716/2, longitudinal section through a row of laterals, x 19.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sufficient to give a reasonable representation of a species (Dixon 1974: 568; Scrutton 1989: 40; Mõtus: 2004, etc.). Unfortunately skeletal characters are not explained and biometrically defined properly in older taxonomic papers. Often discrimination of different species was based on corallite size using only the most common interval of the corallite diameter. Likewise the spacing interval between tabulae was used, a feature which is considered nowadays to be highly variable ecophentotypically (Mõtus 2005: 27).

The following parameters are measured or counted on thin sections:

Pachyfavositids and Thamnoporids:

Average corallite dimensions (CD): these parameters are calculated by measuring corallite cross-sections at right angles to one another between corallite midwalls (Sutton 1966; Young & Elias 1995). For corallites which are not equidimensional, the axis dividing the corallite into two bilaterally symmetrical parts is used to orient the first measured dimension.

Corallite area (CA): corallites within an area of 1 cm^2 of a corallum cross section are counted. Half and quarter corallites are included in the count. The mean corallite area, in mm^2, is calculated from the inverse of this count (Young & Elias 1995).

Wall thickness (WT): the thickness of each shared corallite wall is measured between septa, where it is less affected by thickening.

Pore diameter (PD): the diameter of pores is measured in cross sections

Number of tabulae in 5 mm (T5): the number of tabulae in 5 mm is counted along the corallite axis. Counting directly starts over one tabula along a 5 mm interval without the starting tabula.

Alveolitids:

Corallite dimensions: length (L) and width (W) of alveolitid corallites are measured separately because most alveolitid corallites are ovate in transverse section. Dark lines are reduced therefore measurements are done from wall to wall.

Length: width index of corallit cross section (L:W): ratio of axes of corallite diameters are calculated.

Corallite area (CA): investigational processing described above.

Wall thickness (WT): the thickness of corallite wall is measured in longitudinal sections.

Pore diameter (PD): see above.

Number of tabulae in 5 mm (T5): see above.

Heliolitids:

Tabularium diameter (TaD): measurement is done internally from wall to wall where walls are least thickened by septal development.

Tubule diameter (TuD): internal diameter of each coenenchymal tubule is measured.

Tabularium area (TA): the tabularium area is calculated from the diameter.

Wall thickness (WT): thickness of the tabularium wall is measured between septa, where it is least affected by trabecular thickening.

Number of tabulae in 5 mm (T5): see above.

Class **Anthozoa** Ehrenberg, 1834

Order **Favositida** Wedekind, 1937

Suborder **Favositina** Wedekind, 1937

Family Favositidae Dana, 1846

Subfamily Favositinae Dana, 1846

Genus *Pachyfavosites* Sokolov, 1952

Type species: *Calamopora polymorpha* var. *tuberosa* Goldfuss, 1829, p. 74, pl. 27, fig. 2a, from the Middle Devonian, Germany.

Diagnosis. Colony cerioid semicircular, nodular, flat, or irregular composed of polygonal prismatic corallites with closely adjoining double walls and nearly always with distinct suture. Corallite lumen rounded or rounded polygonal in cross sections. The double walls are pierced by one or two vertical rows of pores. Septal spines projecting from the walls are arranged in longitudinal rows. Tabulae thin, horizontal and mostly complete. Reproduction by lateral increase.

Remarks. *Pachyfavosites* was erected by Sokolov (1952: 43-44) – primarily established as a subgenus of *Favosites* – for favositids with a certain "tendency for the creation of rounded inner corners". Lütte (1993: 57) recognized a great variability of colony shapes and internal structures of *P. polymorphus* showing transitions to *Thamnopora cervicornis* (Blainville, 1830) and *Pachyfavosites cronigerus* (Orbigny, 1850). The latter seems to be however only an ecologically caused variant of *P. polymorphus* (see Birenheide 1985: 68; Lütte 1993). Oekentorp (1969: 259-264, 1975: 64-67) also pointed out similarities between the two species *P. cronigerus* and *P. polymorphus* but regarded the first as a subspecies of the second. According to the intra- and interspecific variability of both internal skeletal structures and coral shape we support the idea of a certain ecoplasticity of *P. polymorphus* that makes the differentiation of *P. cronigerus* dispensable.

Pachyfavosites polymorphus (Goldfuss, 1829)

Pl. 2, figs 1, 2

Material. Sample CK 644: six specimens, seven thin sections CK644/6-12); MPUM 9717/1-7; Shogram Fm., upper Givetian.

Sample CK35: two thin sections CK35/1-2. MPUM 9718/1-2, Debris sample, Upper Yarkhun Valley.

Description. Coralla spherical to bulbous, 25 x 30 mm to 80 x 60 mm in dimension. Corallites polygonal, differentiated in size, large corallites are the dominating ones, the common diameter is 0.9-1.20 mm. The double

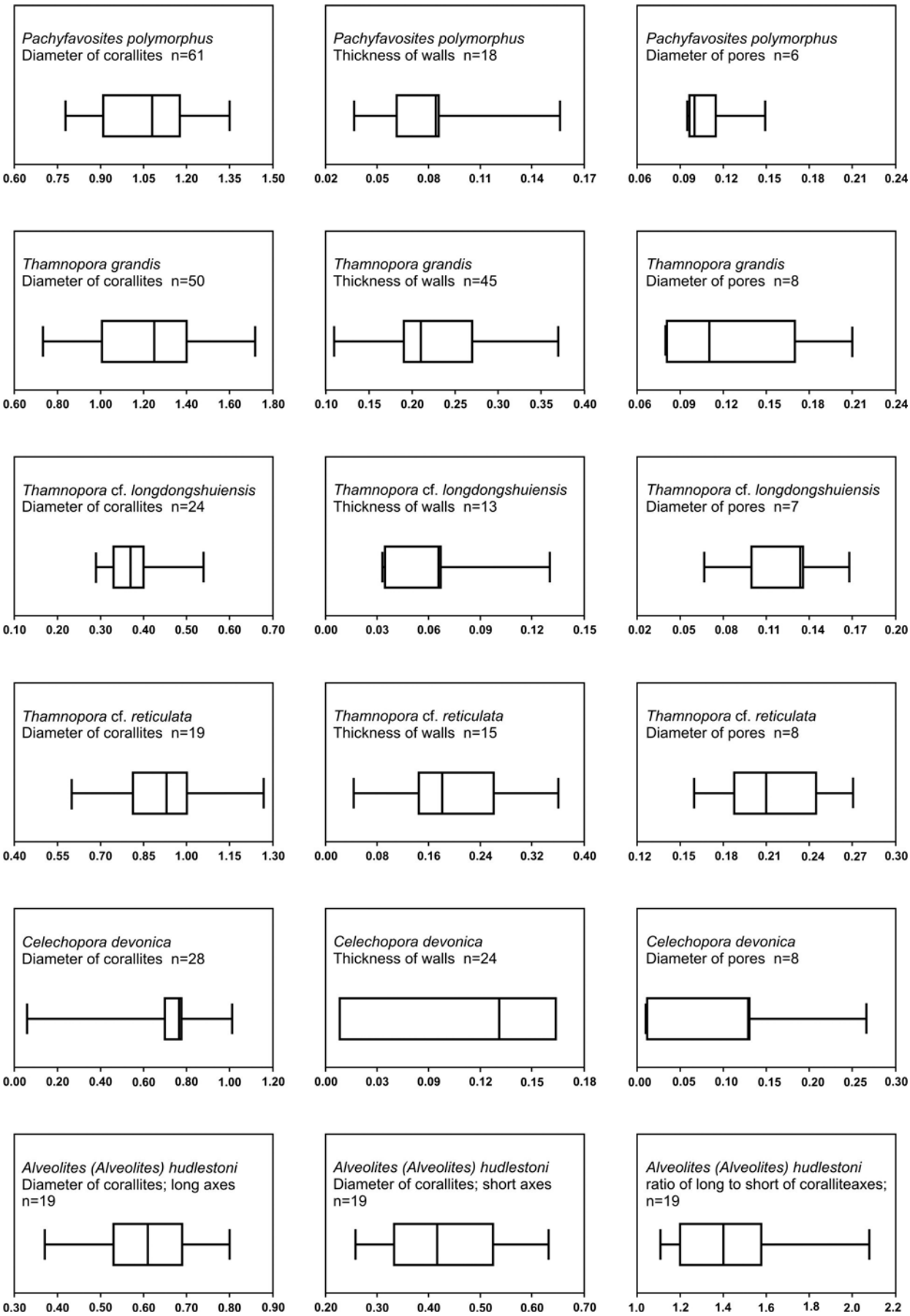


Fig. 5 - Box-plots with median values (black squares), lower and upper quartiles (terminations of the box) and whiskers (minimum and maximum values) of biometric data.

wall is straight and has no well developed septal spines. The wall thickness is about 0.64-0.85 mm. Rare mural pores are about 0.11 mm in diameter. Tabulae horizontal or slightly concave, mutual distance 3.08-3.87 mm. As an average 9-11 tabulae are found at a 5 mm interval.

Morphometric data. Measuring data derived from seven small colonies (Fig. 5).

	Number of measure-ments	maximum value	minimum value	median value	Mean	standard deviation
CD	61	1.35 mm	0.78 mm	1.09 mm	1.04 mm	0.232
WT	18	0.16 mm	0.43 mm	0.85 mm	0.83 mm	0.024
PD	6	0.15 mm	0.10 mm	0.11 mm	0.11 mm	0.021

CA: 0.0118 - 0,0091 mm^2

Discussion. In contrast to corallite dimensions given by Birenheide (1985) for *Pachyfavosites polymorphus* colonies found in Germany, biometric data of specimens studied show slightly smaller dimensions.

Geographical and stratigraphical distribution. *Pachyfavosites polymorphus* was recorded from the Givetian of Europe and possibly North-Africa (May 1993 cum lit.), Western Sibiria (Cernyshev 1951; Dubatolov 1959) and South China (Oekentorp & Deng 1989; Yang et al. 1978, etc).

Subfamily Pachyporinae Gerth, 1921

Genus *Thamnopora* Steininger, 1831

Type species: *Thamnopora madreporacea* Steininger, 1831 [= *Alveolites cervicornis* Blainville, 1830], Steininger, 1831, p. 11; from the Middle Devonian of the Eifel District, Germany.

Diagnosis. Colony massive, ramose, reticulate or branching with rounded polygonal calices oriented ± perpendicularly to the corallum surface. Corallites arranged fan-like, frequently strongly increasing diameters and wall thickness during individual growth. Diameters of corallites between 0.3 mm and 3 mm. Double walls may be pierced by vertical rows of pores. Septal spines numerously to not detectable; normally squamulae and septal combs are missing. Tabulae, developed frequently to rare, are thin, complete, horizontal. Reproduction by lateral increase.

Thamnopora grandis Dubatolov, 1959

Pl. 2, figs 3, 4

Material. Sample CK 472: four specimens. Five thin sections CK472/1-5. MPUM 9719/1-5. Shogram Fm., Chillinji section, upper Givetian.

Sample CK 474: one specimen. Two thin sections CK474/1-2. MPUM 9720/1-2. Shogram Fm., Chillinji section, upper Givetian.

Description. Colonies are fascicular, with cylindrical branches 15 to 18 mm in diameter. In transverse section the corallites are polygonal, with round or suboval lumen. The diameter of corallites is axially about 1.25 mm and may increase peripherally up to 1.5 mm and more. In longitudinal sections the corallites of the axial zone are vertical and ached in the peripheral zone. The microstructure of the walls is fibro-lamellar, the dark median suture is distinct. The thickness of the walls is about 0.21 mm axially (median value of measured dimensions) and also increase peripherally noticeably. The calices are deep and funnel-like. Tabulae are thin and horizontal, mostly 8 countered at a 5 mm interval. The mural pores are round, arranged in a single row, and of 0.1 to 0.2 mm in diameter. Septal spines are very poorly developed.

Morphometric data. Measuring data derived from 5 thin sections CK472/1-5 (Fig. 5).

	Number of measure-ments	maximum value	minimum value	median value	Mean	standard deviation
CD	50	1.72 mm	0.74 mm	1.25 mm	1.23 mm	0.209
WT	45	0.37 mm	0.11 mm	0.21 mm	0.23 mm	0.056
PD	9	0.21 mm	0.08 mm	0.11 mm	0.14 mm	0.058

Discussion. The specimens studied accurately concur with the original description of the species although biometric information is meagre.

Geographical and stratigraphical distribution. *Thamnopora grandis* is known from the lower to middle Devonian of Russia.

Thamnopora cf. **longdongshuiensis** Deng, 1979

Pl. 3, figs 1, 2; Fig. 6

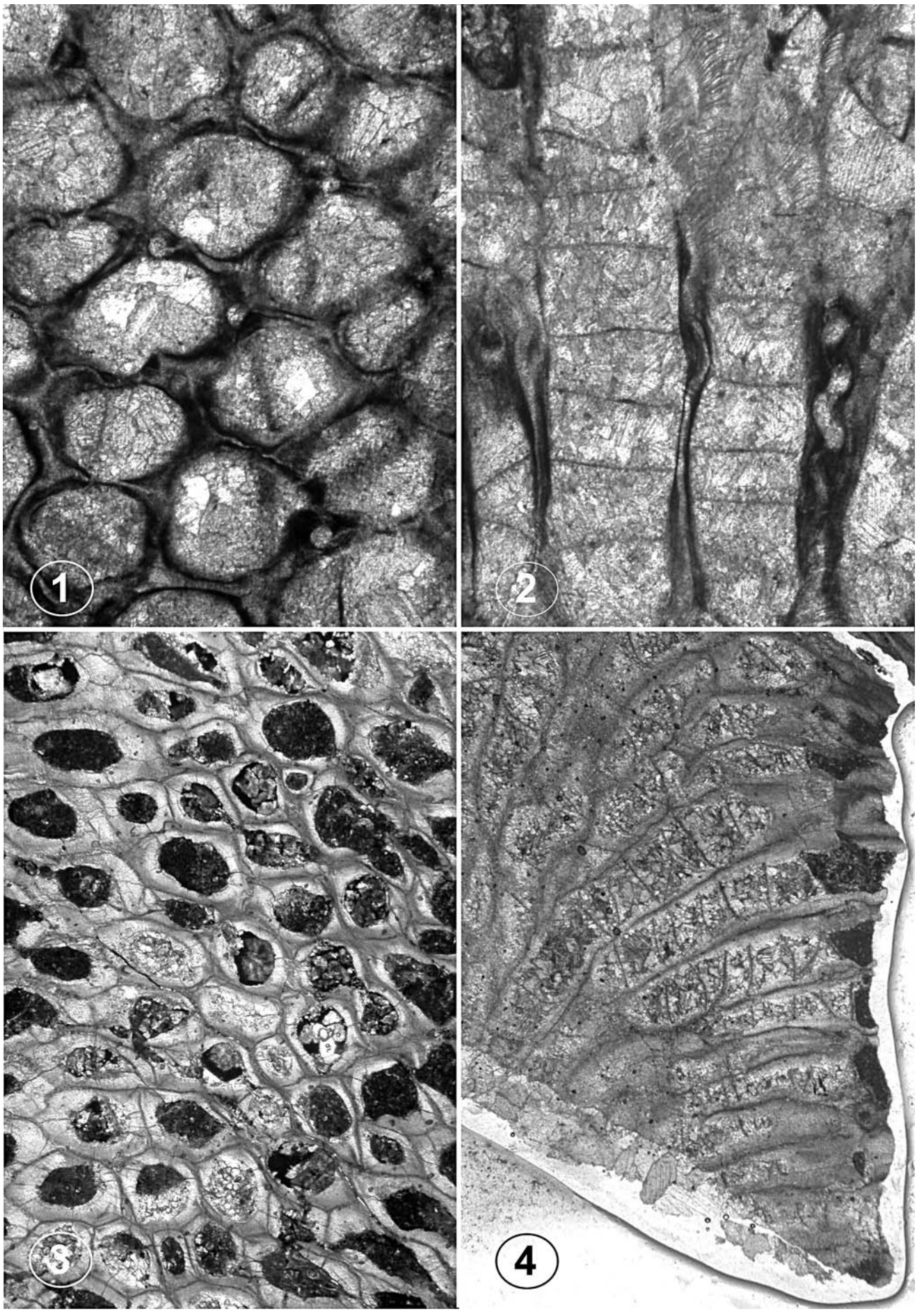
Material. Sample KK 764: 11 specimens in different orientation. Thin sections KK764a, KK764b/3-4, KK764c/1-2. MPUM 9721/1-5. Additional thin-sections: MPUM 9715/1-2. Chilmarabad Fm., middle Devonian (Eifelian?)

Description. Small sized branches up to approx. 25-30 mm length and 30 - 45 mm in diameter. Corallites polygonal, their common diameter is about 0,4 mm. Bad preservation restricts statements on wall structures and development of septal spines. Wall thickness was detected by using illumination by darkfield condensator and is about 0.05-0.10 mm. Mural pores are about 0.13 mm in diameter. Tabulae horizontal, their spacing distances are not detectable due to bad preservation.

PLATE 2

Fig. 1-2 - *Pachyfavosites polymorphus* (Goldfuss, 1829)
1: MPUM 9717/3, cross-section, x 18; 2: longitudinal section, note helicoidal structure of *Helicosalpinx* (compare with pl. 5, figs. 3-6), x 27.5

Figs. 3-4 - *Thamnopora grandis* Dubatolov, 1959.
3: MPUM 9719/1, cross-section through the outer part of a branch with thick corallite walls, x 12; 4: MPUM 9719/3, longitudinal section, x 12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Morphometric data. Measuring data derived from three thin sections (Fig. 5).

	Number of measure-ments	maximum value	minimum value	median value	Mean	standard deviation
CD	24	0.54 mm	0.29 mm	0.37 mm	0.38 mm	0.066
WT	13	0.13 mm	0.03 mm	0.06 mm	0.06 mm	0.035
PD	7	0.17 mm	0.07 mm	0.13 mm	0.12 mm	0.033

Discussion. The reliability of biometric data is limited because of preservation. However, the specimens are characterized by small external (corallum) and internal (corallites) skeletal dimensions that resemble on those of *Thamnopora longdongshuiensis* described by Deng (1979: 155). from the Eifelian of South China.

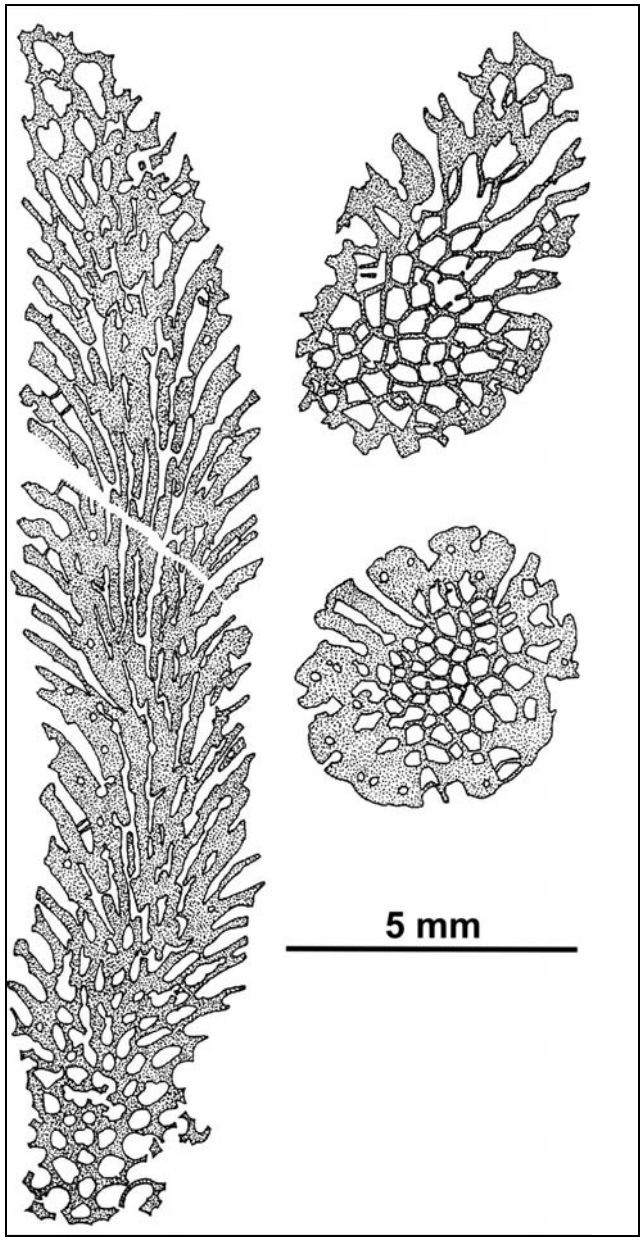


Fig. 6 - Skeletal arrangement of *Thamnopora* cf. *longdongshuiensis*; left: longitudinal section, right: oblique and cross-section of a branch (after MPUM 9721/1 and MPUM 9721/4).

Geographical and stratigraphical distribution. *Thamnopora longdongshuiensis* is so far known from the (upper?) Eifelian of Dushan district (Guizhou/ South China).

Thamnopora cf**. reticulata** (Blainville, 1830)

Pl. 3, figs 2, 3

Material. Sample CK 377: seventeen fragments of branches, two thin sections CK377/1 (longitudinal section), CK 377/2 (cross-section). MPUM 9722/1-2. Shogram Fm., (upper?) Givetian.

Description. Anastomosing to parallel branches; fragments up to 45 mm in length a with diameters of 10-15 mm. Corallites polygonal, the common diameters about 0.9 mm. The double wall is straight and show very rare septal spines. Wall thickness about 0.20 mm; mural pores are about 0.20 mm in diameter. Tabulae horizontal or slightly concave.

Morphometric data. Measuring data derived from one colony (Fig. 5).

	Number of measure-ments	maximum value	minimum value	median value	Mean	standard deviation
CD	19	1.27 mm	0.60 mm	0.93 mm	0.88 mm	0.194
WT	15	0.37 mm	0.05 mm	0.19 mm	0.21 mm	0.084
PD	13	0.27 mm	0.16 mm	0.21 mm	0.20 mm	0.041

Discussion. Although biometric data show close similarities with *Thamnopora reticulata* (Blainville, 1830) the specimens studied differ by rarely developed septal spines and insufficient developed tabulae (confer description of *T. reticulata* by Brühl 1999: 43-44).

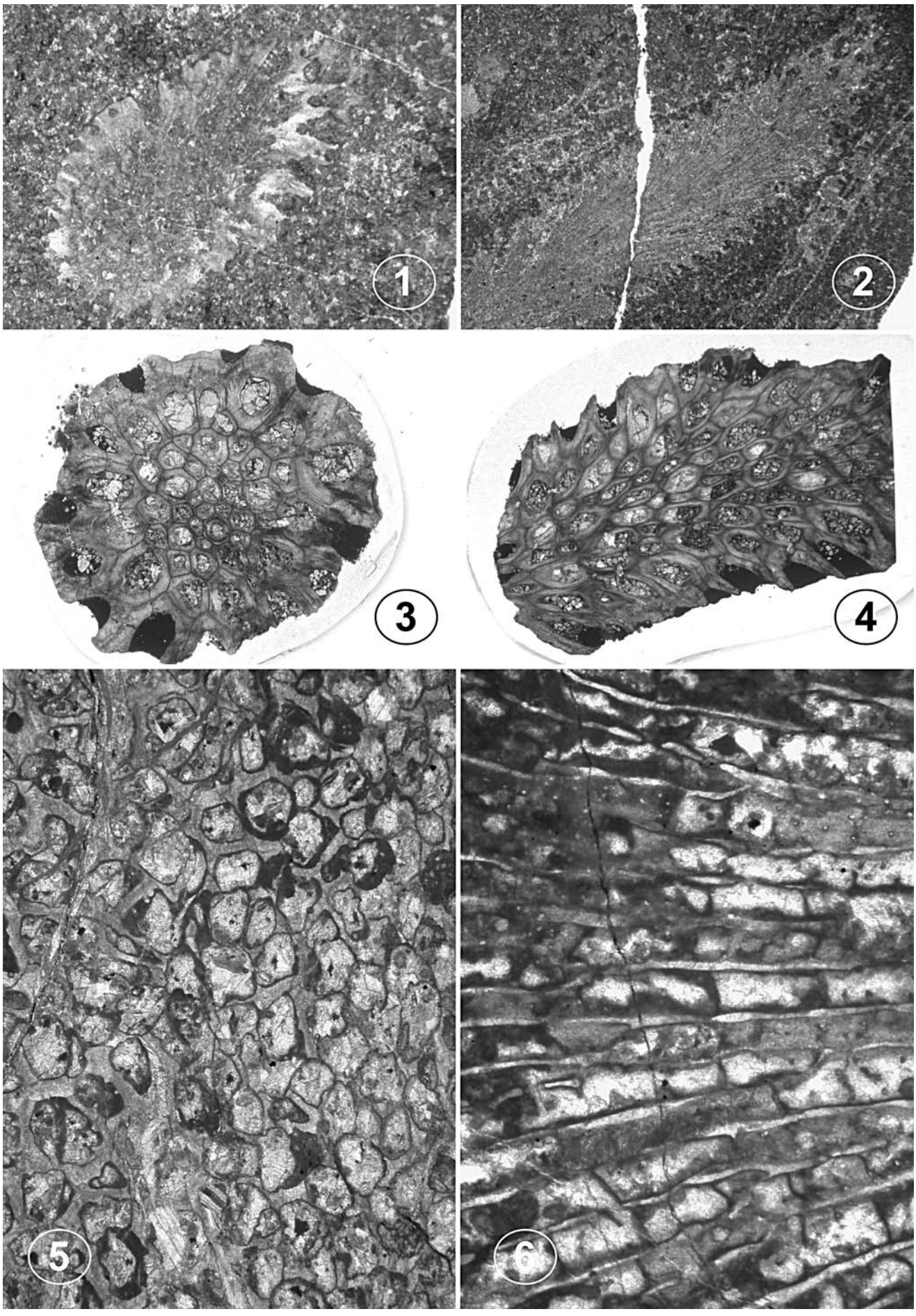
Geographical and stratigraphical distribution. *Thamnopora reticulata* is well distributed in the Givetian of Europe, China and Russia (cf. Kropfitsch & Schouppé 1953, Brühl 1999, etc.) and was also described by Schouppé (1965) from Kuragh (Chitral).

PLATE 3

Fig. 1-2 - *Thamnopora* cf. *longdongshuiensis* Deng, 1979.
1: MPUM 9721/4, cross-section through branch, x 8.5; 2: longitudinal, slightly oblique section through a branch, x 10.5.

Figs. 3-4 - *Thamnopora* cf. *reticulata* (Blainville, 1830)
3: MPUM 9722/2, cross-section through an isolated steam, x 7.6; 4: MPUM 9722/1, longitudinal section, x 5.4.

Figs. 5-6 - *Celechopora devonica* (Schlüter, 1885).
5: MPUM 9723/2, cross-section a branch, x 16.3; 6: MPUM 9723/1 longitudinal section, x 16.3.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Genus *Celechopora* Pradáčová, 1938

Type species: *Celechopora kettnerae* Pradáčová, 1938

Diagnosis. Thin-branched colonies with corallites predominantly inclined to the surface of the branches. Calices may have rhomboid outlines; width greater than height. Squamulae may be developed only in distal parts of corallites. Septal spines ?absent. Tabulae thin; mural pores scarce. Walls thicken slightly distally.

Celechopora devonica (Schlüter, 1885)

Pl. 3, figs 5, 6

Material. Sample CK 853: several fragments of branches in six thin sections. For taxonomical determination: two thin sections CK853/1 (longitudinal section), CK853/2 (cross-section). MPUM 9723/1-2. Tash Kupruk dolostones, upper Givetian?

Description. Fragments of branches about 35 mm in length and 15 mm in width. Polygonal corallites arranged oblique to the surface with common diameters about 0.70 to 0.75 mm. In longitudinal sections well developed septal spines and squamula are visible. Wall thickness about 0.13 mm; mural pores range in their diameters between 0.10 and 0.27 mm. Tabulae horizontal or slightly concave; distances between tabulae about 1.0 mm.

Morphometric data. Measuring data derived from one colony (Fig. 5).

	Number of measurements	maximum value	minimum value	median value	Mean	standard deviation
CD	28	1.03 mm	0.63 mm	0.73 mm	0.66 mm	0.266
WT	24	0.17 mm	0.10 mm	0.13 mm	0.14 mm	0.029
PD	13	0.27 mm	0.10 mm	0.13 mm	0.14 mm	0.043

Remarks. Biometric data indicate close similarities with specimens described from the upper Givetian of Germany by Byra (1983) and Birenheide (1985).

Discussion. The studied coralla show some differences with "typical" *Celechopora* colonies known from the European region especially concerning arrangement of pores and spines. According to the friendly communication of J. Hladil (March 2007) the regularity and dimensions of mural pores is not characteristic of the genus. Likewise the presence of septal spines is atypical since *Celechopora* show a prevalence of smooth corallite walls.

Geographical and stratigraphical distribution. *Celechopora devonica* is known from the upper Givetian of Western Germany and Czech Republic (Moravia).

Suborder **Alveolitina** Sokolov, 1950

Family Alveolitidae Duncan, 1872

Subfamily Alveolitinae Duncan, 1872

Genus *Alveolites* Lamarck, 1801

Type species: *Alveolites suborbicularis* Lamarck, 1801, p. 375 (Nicholson & Etheridge 1877, p. 356)

Diagnosis. Corallum massive, extensiform, encrusting, in some with irregular or fingerlike outgrowths; corallites slender, in cross section crescentic, triangular, rounded- or compressed-polygonal or meandroid; corallites commonly inclined, with upper wall arched and lower applied to the substrate; opening to surface at acute or less commonly almost at right angle, in compressed-rounded calices; walls of varying thickness, microstructure radially fibrous with growth lamellation; alternately light and dark pigmented growth zones common; pores uniserial, on narrow sides of corallites; septal spines small, thin, commonly one row of larger spines related to longitudinal increase; tabulae horizontal, thin and complete, inclined or somewhat curved; increase lateral.

Remarks. During the last two decades a debate on the range of *Alveolites* took place among authors that split up the genus into several independent genera (e.g. Iven 1980; Lin et al. 1988, etc.) and others (e.g. Byra 1983; Birenheide 1985) integrating different form variants into the genus *Alveolites* without identifying subgenera. To the contrary, May (1993: 143-144) distinguished the following subgenera: *A. (Alveolites)* Lamarck, 1801; *A. (Alveolitella)* Sokolov, 1952; *A. (Crassialveolites)* Sokolov, 1955 and *A. (Tetralites)* Mironova, 1970. The discrimination of subgenera is mainly based on differing growth habits of the coralla. However, this attribute might rather mirror ecologic aspects of the environment than genetic facets.

Alveolites hudlestoni Reed, 1922

Pl. 4, figs 1, 2

Material. Sample CK 644: 5 specimens. Five thin sections CK664/1-5. MPUM 9724/1-5. Shogram Fm., upper Givetian.

Sample CK 371: one specimen. One thin section CK371/1. MPUM 9725. Shogram Fm., upper Givetian.

Sample CK 377: two specimens. Two thin sections CK377/3-4. MPUM 9726/1-2. Shogram Fm., upper Givetian.

Sample CK 718: one specimen. Two thin sections CK718/1-2. MPUM 9727/1-2. Shogram Fm., upper Givetian.

Sample KK 773: two specimens. Two thin sections KK773/1-2. MPUM 9728/1-2. Shogram Fm., upper Givetian.

Sample CK 500: two specimens. Two thin sections CK500/1-2. MPUM 9729/1-2. Debris sample in the scree north of Zhoe Wurt.

Description. Species of *Alveolites* with subglobular colonies built up by multiplicate overgrowing parts within the corallum and only meagrely developed septal spines. Corallum shape: incomplete colonies are hemispheric to subglobular; maximum height 60 mm; diameter of maximally 90 mm. Surface areas more or less smooth with small calices squeezed together; sometimes an eddy-like striation is visible which corresponds with longitudinally cuttings of corallites. Besides frequently a change of bright and dark concentric layers is visible.

In thin-sections colonies often consist of bundles of corallite tubes that bend all-side outward from the centre. During growth corallites often change their direction; individual parts of the corallum may even perpendicularly turn off from their original growth direction and overgrow neighbouring parts. This particular

growth habit implies different increase rate in the individual sections of the corallum. Corallites are squeezed together and show irregularly polygonal to semilunar cross sections. The larger diameter is on average 0.7-0.8 mm, smaller about 0.5 mm. Wall thickness may vary considerably. Boundaries between neighbouring corallites are more clearly developed in longitudinal sections than in cross section due to a more clearly developed dark line.

Sometimes small pin-shaped septal spines occur, which rise up individually from the lower, more or less straight wall into corallite space. The very rare wall pores, 0.1-0.15 mm in diameter, are arranged in single-rows. Tabulae are thin, predominantly horizontal; distances among them may change in an interval of 0.2-0.8 mm.

Morphometric data. Measuring data derived from one thin section (Fig. 5).

	Number of measure-ments	maximum value	minimum value	median value	Mean	standard deviation
L	19	0.80 mm	0.37 mm	0.61 mm	0.60 mm	0.114
D	19	0.64 mm	0.27 mm	0.42 mm	0.44 mm	0.108
L:W	19	2.09	1.11	1.40	1.43	0.277
WT	5	0.21 mm	0.06 mm		c. 0.11 mm	
PD	5	0.15 mm	0.10 mm			

CA: c. 0.003 mm^2

Discussion. Reed (1922) described *Alveolites suborbicularis* var. *hudlestoni* from the Koragh ridge and from "Shugram, opposite Reshun" (Reed 1922: 23). For separating the new subspecies from *A. suborbicularis,* Reed (1922) pointed out the different growth form, the "more polygonal and less compressed shape of corallites". Likewise Schouppé (1965: 47) highlighted the special growth habit of *A. hudlestoni* which is comparable with *A. edwardsi* and argued for an independent species. Although a large agreement exists in the growth form with *A. edwardsi*, the Chitral specimens however differ by the smaller extents of the colonies, the more meagrely developed septal spines and the thicker walls.

Geographical and stratigraphical distribution. *Alveolites hudlestoni* is only known from middle to Upper Devonian of the lateral extension of the Northern Karakorum Terrain in Chitral (Reed 1922; Schouppé 1965).

Order **Heliolitida** Frech, 1897
Suborder **Heliolitina** Frech, 1897
Family Heliolitidae Lindström, 1876

Explanatory note. Concepts of the classificatory system of heliolitid corals have changed several times throughout the history of the paleozoology of corals (cf. Hubmann 1997). The differences in conceptions affect not only the higher systematic categories but also the delimitation and range of the single genus and its familial assignment (e.g.: Hill 1981 vs. Bondarenko 1992).

Genus *Heliolites* Dana, 1846

Type species: *Astraea porosa* Goldfuss (1826, p. 64, pl. 21, fig. 7a-g) from the Middle Devonian of the Eifel District, Germany.

Diagnosis. Heliolitidae with cylindrical corallites in coenenchyme of prismatic tubules; corallite walls smooth, faceted or longitudinally plicate; tabularia frequently with 12 septal spines of various lengths; tabulae mostly complete, horizontal; coenenchymal tubules with mostly complete horizontal diaphragms.

Discussion. Dixon (1996, 1998) interprets the genus *Heliolites* again in a more traditional sense, as a widely occurring Ordovician to Devonian genus, and not restricted, as proposed by Bondarenko (1992, p. 100-102), to the few Lower and Middle Devonian species with septal laminae of two orders.

Heliolites? sp.

Pl. 4, figs 3, 4

Material. Sample CK 371: one specimen. Two thin sections CK371/2-3. MPUM 9730/1-2. Shogram Fm., (upper?) Givetian.

Description. Cylindrical-rounded colony about 10 cm in diameter and 4-5 cm high. Very small sized corallites range between 0.29-0.31 mm (mean 0.26 mm) in diameter; walls commonly similar in thickness to walls of coenenchymal tubules. Septal spines not detectable. Corallites extraordinary densely distributed in coenenchyme: up to 650 corallites per cm^2 in cross section. Corallite centres in average 0.45 mm apart; 1-3 rows of coenenchymal tubules between corallites. Coenenchymal tubules mostly regular, polygonal in cross section, 0.08-0.10 mm (mean 0.09 mm) in diameter. Tabulae and diaphragms mostly complete, flat. Spacing of adjacent tabulae and diaphragms different (approx. 5 times more frequently in diaphragms). No cyclomorphic growth zonation.

Morphometric data. Measuring data derived from one thin section.

	Number of measurements	maximum value	minimum value	Mean
TaD	23	0.31 mm	0.29 mm	0.26 mm
TuD	30	0.10 mm	0.08 mm	0.09 mm
WT	5	0.05 mm	0.04 mm	

Discussion. The specimen is moderately to bad in preservation and therefore excludes investigations of fine wall structures. The presence of the very small

and densely packed corallites casts an assignment to *Heliolites* into doubt.

Genus *Pachycanalicula* Wentzel, 1895

Type species: *Heliolites barrandei* Penecke (1887, p. 271-272, pl. 20, figs. 1-3) from the Middle Devonian of the Graz Palaeozoic, Austria.

Diagnosis. Heliolitidae with cylindrical corallites in coenenchyme of rounded polyhedral tubules; corallite walls smooth, faceted or longitudinally plicate; tabularia with 12 septae consisting of short longitudinal stripes with upwards directed spines on their free endings; they widen into a slight club shape on their distal point; tabulae complete, horizontal; coenenchymal tubules with complete horizontal diaphragms.

Discussion. There are different opinions regarding the validity of the genus *Pachycanalicula* (e.g.: Lang et al. 1940; Sokolov 1955; Lin et al. 1988; Bondarenko 1992 and previous papers) and its synonymy with *Heliolites* Dana, 1846 (e.g.: Lindström 1899; Lecompte 1952; Flügel 1956; Birenheide 1985). However, the main reason for diverged systematic opinions views was the inadequate knowledge of the type species itself. The characteristic septal spines are an important generic level character: They developed "on their inner free border strong spines, which are directed obliquely upwards" (Hubmann 1997).

Pachycanalicula? sp.

Pl. 5, fig. 1

Material. Sample KK 764: one specimen. One thin section (cross-section); KK764d. MPUM 9731. Chilmarabad Fm., middle Devonian (Eifelian?).

Description. Corallites with septal spines 1.28-1.79 mm in diameter. Coenenchyme consists of prismatic tubules, mainly polygonal-rounded in cross section; average tubule diameters 0.45 mm; walls 0.04-0.05 mm thick, generally similar to corallite wall thicknesses.

Morphometric data. Measuring data derived from one thin section.

	Number of measurements	maximum value	minimum value	median value	Mean	standard deviation
TaD	26	1.79 mm	1.28 mm	1.45 mm	1.44 mm	0.129
TuD	17	0.29 mm	0.23 mm	0.23 mm	0.24 mm	0.022
WT	3	0.05 mm	0.04 mm			

Discussion. Although due to the lack of a longitudinal section an exact determination is impossible axial structures in the corallites suggest the presence of "Columellardornen" ('columellar spines') in the sense of Birenheide (1985: 9) is a typical feature of *Pachycanalicula*.

"*Caunopora* Phillips, 1841"

Type species: *Caunopora placenta* Phillips (1841, p. 18, pl. 10, figs. 28 a-d) from the Givetian of "Bergisches Land", Germany.

Diagnosis. Colonies of Syringoporidae with small long-cylindrical and thin-walled corallites in-grown into platy and spherical stromatoporoids. Connecting tubules and septal spines are rare to missing. Tabulae irregularly infundibuliform, sometimes concave or horizontal.

Remarks. According to ICZN, the genus *Caunopora* is invalid since it concerns the intergrowing phenomenon of different organisms (i.e. stromatoporoids and syringoporid tabulates and not a single taxon. Moreover, the type material is lost (Birenheide 1985: 135) and descriptions and illustrations on *Caunopora placenta* by Bargatzky (1881) and Lecompte (1951-1952) indicate that different stromatoporids (*Stromatopora* Goldfuss, 1826 and *Stromatoporella* Nicholson, 1886) containing three different species of syrigoporid tabulates are summarized.

However, "*Caunopora*" is used herein as an informal term for an association of stromatoporoid coenostea intergrown with syringoporids that may either be interpreted as commensalism (e.g. Mistiaen 1984; Kershaw 1987) or as symbionts (Cernyshev 1951; Cudinova 1986; Young & Noble 1990). The syringoporid corals apparently benefited from growth interaction due to the fact that their fragile corallites were well-protected from water agitation.

"Caunopora" sp.

Pl. 5, fig. 2

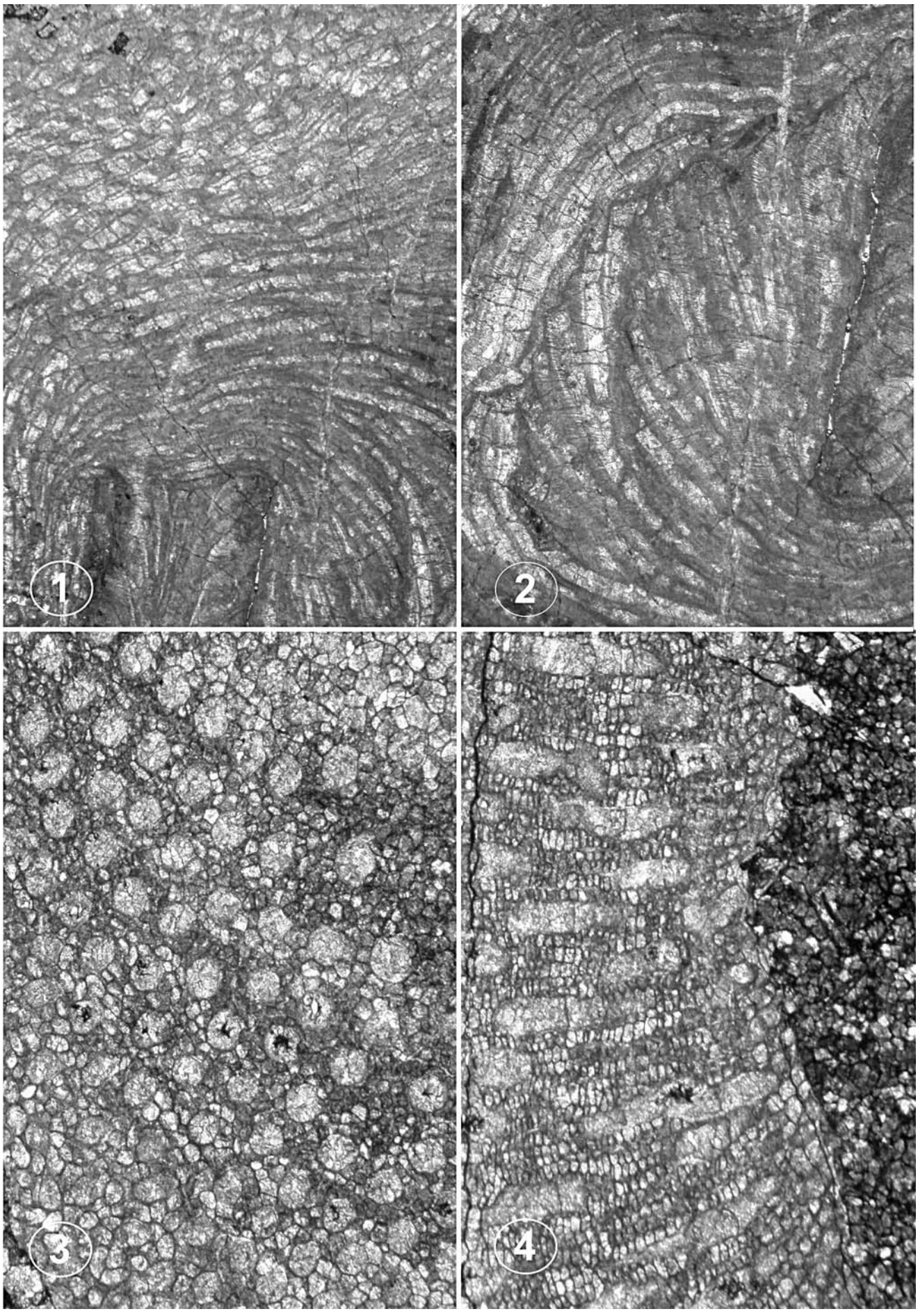
Material. Sample KK 765: one longitudinal thin section. MPUM 9732. Chilmarabad Fm., middle Devonian (Eifelian?).

Description. Syringoporidae corallites arranged vertical to growth direction of the hosting stromatoporoid; diameters of corallites 0.07-0.11 mm (mostly 0.075 mm). Connecting tubules about 0.04 mm in diameter including walls. Due to recrystallisation neither the ar-

PLATE 4

Fig. 1-2 - *Alveolites (Alveolites) hudlestoni* Reed, 1922.
1: MPUM 9724/1, section through the inner part of a colony encrusting a branching tabulate, x 10; 2: longitudinal section of a "self-encrusting part of the corallum, x 12.

Figs. 3-4 - *Heliolites?* sp.
3: MPUM 9730/2, cross-section through coenenchymal corallum with corralites aranged in rows, x 19; 4: MPUM 9730/1, longitudinal section of the corallum, x 19.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rangement of the tabulae within the long-cylindrical and thin-walled corallites nor the character of the stromatoporoid can be detected.

Trace fossils

Within corals, tubelike vermiform inclusions are known since a long time. Among them the most spectacular is the Middle Devonian *Hicetes* "worm" in the tabulate *Pleurodictyum* (Clarke 1908). Apparently this association is a typically host-specific association. However, a number of different tabulates exhibit tubes within their walls or lumina that are straight or coiled exhibiting no internal structures, or show tabulae. In comparison to modern corals in which endosymbionts living inside the skeleton is common (e.g. polychaete worms, pyrgomatid barnacles, vermetid gastropods, and bivalves) tubelike structures in tabulates are interpreted as living spaces. Endosymbiont organisms live within the growing skeletons of living host organisms producing cavities which are called bioclaustrations.

Contrary to boring organisms which excavate into skeletal material, bioclaustration cavities are produced around an endosymbiont by the host organism itself. The inter-coordinated growth of both, the host and the endosymbiotic organism led to the introduction of a new ethological category called impedichnia by Tapanila (2005). Endosymbionts may locally inhibit normal skeletal growth of the host, and contrariwise accelerated growth rate of the hosting coral produces – in the case of the coiled *Helicosalpinx* – a straighter spiral of the tubes.

Helicosalpinx asturiana Oekentorp, 1969

Type species: *Helicosalpinx concoenatus* (Clarke, 1908) (= *Streptindytes concoenatus* Clarke, 1908, p. 158, pl. 1, figs. 5,6) from the Upper Silurian of the Cobleskill Limestone, Northern America.

Pl. 5, figs 3-6

Material. Individuals of this trace fossil are found in the skeletons of *Pachyfavosites polymorphus* described herein. Shogram Fm., upper Givetian and Debris sample, Upper Yarkhun Valley.

Diagnosis. Helicoidal traces, specifically located in the corners of the corallites of tabulates. Calcareous wall linings were not secreted by the individual itself but by the host organism (Stel 1976).

Description. Ovate to kidney-shaped cuts of worm tubes are recognisable in sections vertical to the growth direction of coral colonies. In longitudinal sections convoluted tubes with up to 4-5 windings per 1 mm can be found. Both sinistral (upwardly coiling clockwise) and dextral (upwardly coiling anticlockwise) spiraling occurs. The diameter of the tubes is constantly about 0.16 mm. Tube margins are formed by a thin carbonate wall (Hubmann 1991: 44). No tabulae observable within the tubes. Intenseness of spiral growth (dense coiling vs. straight growth) is interpreted as a reflectance on the growth rate of the hosting coral, i.e., faster growth produces a straighter spiral (Stel 1976).

Discussion. In the type material tubes of *H. asturiana* are restricted to the corners of corallites of *Pachyfavosites polymorphus cronigerus*. Oekentorp (1969: 200) recognizes as a "remarkable criterion" that this tubes are only observed in tabulate specimens exhibiting thick walls. Contrary Stel (1976, 1978) and Hubmann (1991) described them located to the direct proximity of the corallite walls which are pierced by the screw-like tubes of *H. asturiana*. The position of the tubes within the host coral seems, however rather be determined by both, the dimension of corallites and thickness of corallite walls. Affected corallites exhibit uninfluenced formations of walls and tabulae suggesting no "defence reactions" of the infected coral against *Helicosalpinx*. Therefore the interpretation of a common nutrition (Oliver 1983: 272) of the tube inhabitants and coral polyps, or more probably different nutritional requirements between the two organisms that fed selectively on different food sources (Tapanila 2004, 2006) becomes more plausible than parasitism.

Geographical and stratigraphical distribution. Recently Tapanila (2005) gave a synoptic review of Palaeozoic bioclaustrations demonstrating a clear frequency of endosymbionts during Givetian times. *Helicosalpinx asturiana* is known from Europe, Russia, Australia, and the Americas (Tapanila 2005).

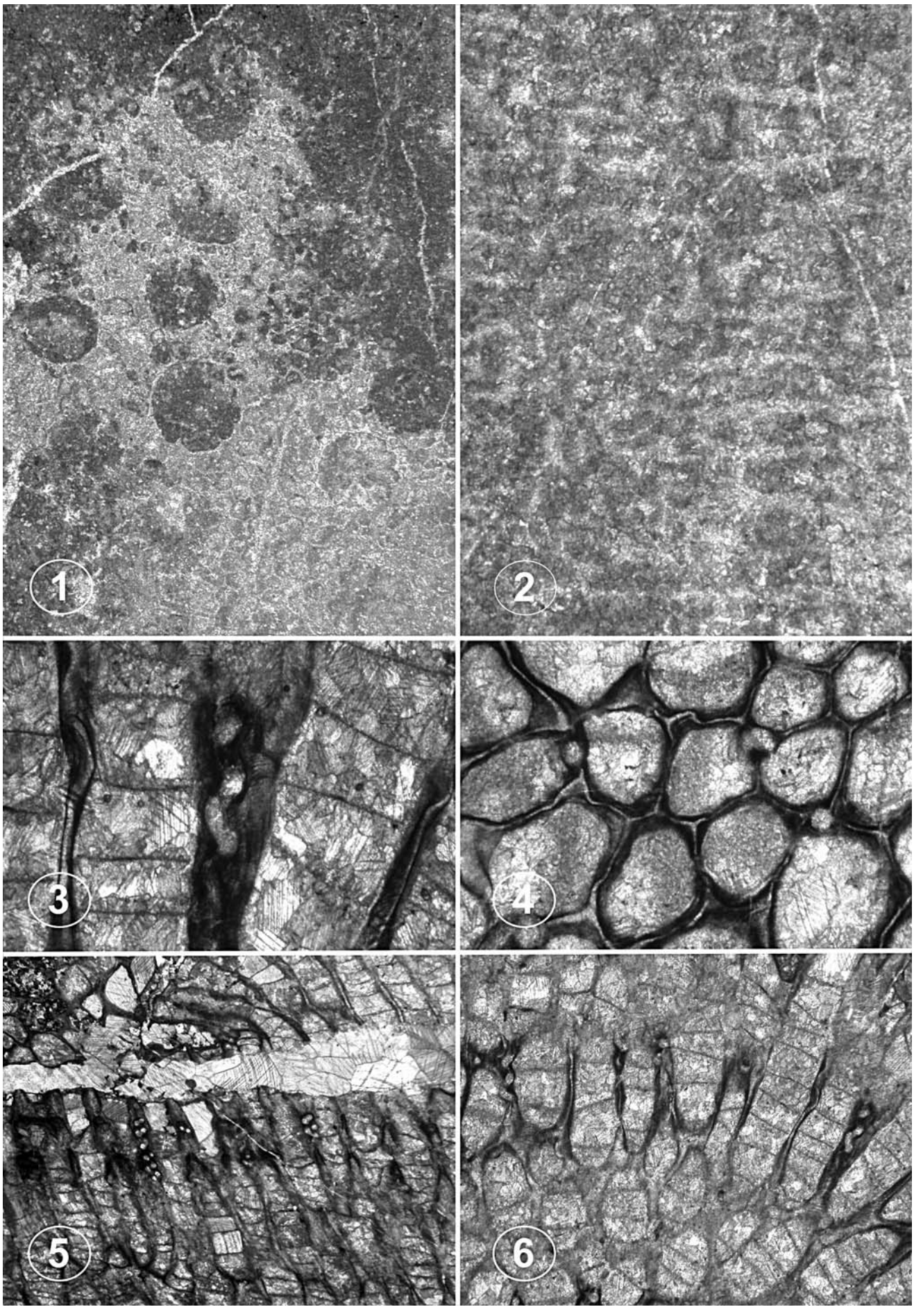
Acknowledgements. We acknowledge the valuable contributions made by the referees Jindrich Hladil and Esperanza Fernández Martínez.

PLATE 5

Fig. 1 - *Pachycanalicula?* sp.
1: MPUM 9731, cross-section through fragment of a corallum, x 9.8.

Fig. 2 - *"Caunopora"* sp.
2: MPUM 9732, longitudinal section through stromatoporoid coenostea with intergrown tabulate tubes, x 38.

Figs. 3-6 - *Helicosalpinx asturiana* Oekentorp, 1969.
3: MPUM 9717/3, longitudinal section of corallites of *Pachyfavosites polymorphus* showing the helicoidal coiled structure of *Helicosalpinx asturiana* within the wall of the coral, x 24.7; 4: cross-sections of corallites with tubes of *Helicosalpinx*, x 6.6; 5, 6: MPUM 9717/2,3, longitudinal sections showing termination of *Helicosalpinx* growth after interruption of coral growth, both x 16.2.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