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DEVONIAN RUGOSE CORALS FROM THE KARAKORUM MOUNTAINS (NORTHERN PAKISTAN)

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Abstract. The Karakorum Block is regarded as a microplate of "Gondwanan" origin and was part of the Cimmerian continent ("Mega Lhasa") which rifted away from the northern margin of Gondwana during the Late Palaeozoic/Early Mesozoic. From the Northern Karakorum Range (Yarkhun and Karambar River Valleys: structurally belonging to the Northern Sedimentary Belt) an Upper Givetian to Lower Frasnian rugose coral fauna of the Shogram Formation is described. The fauna is dominated by cosmopolitan genera such as *Hexagonaria*, *Disphyllum*, *Macgeea* and the *Temnophyllum/Spinophyllum* group, generally showing a geographically wide distribution, although being absent from the Eastern Americas Realm in the Upper Givetian/Lower Frasnian. Therefore its components are of little use for biogeographical deductions at sub-realm level, and in explaining the relation between the Karakorum Range and other Cimmerian crustal blocks. A remarkable exception is the first record of the genus *Pseudopexiphyllum* outside of Turkey, indicating a connection to the western part of the Cimmerides.

On species level, the coral fauna of the Shogram Formation is characterized by the development of a diverse and rather unique fauna including about 35 taxa, that differs from the faunas known from neighbouring crustal blocks. So far, faunistic links to the Central Iranian Microcontinent (Yazd-, and Tabas-Block), the northwest Iranian Plate (Elburz), Central Pamir, the Lhasa Block and Western Qiangtang are not clear, and although each of these fragments are believed to be closely connected they were apparently not in direct contact during the Devonian. However, the Karakorum fauna is remarkably close to one known from the Helmand Block in Afghanistan, showing a very similar generic composition that includes numerous morphologically closely related, although not identical species.

Accordingly, the restricted faunal exchange led to the development of new taxa. Distribution of the new species of *Spinophyllum*, *Pseudopexiphyllum* and *Pseudozaphrentis* is limited to the Karakorum Mountains. Reasons for this individual faunistic development and the missing faunal exchange are unexplained, but suggest that some kind of active faunal barrier must have existed during the Devonian, which led to the development of the specific Karakorum fauna.

With the exception of *Phillipsastrea orientalis* Smith, 1930, which is elsewhere only known from the Burmese Devonian, the occurrence of some other species suggest a connection to regions which are regarded as biogeographically unrelated. A weak relation to central European faunas is indicated by the occurrence of characteristic species of *Macgeea* and *Hexagonaria* known from the Ardennes and the Holy Cross Mountains. More unusual are the faunistic affinities to the Altai-Sayan region shown by the surprising occurrences of species of *Spinophyllum* and siphonophrentid corals morphologically very close to those known from the Altai Mtns. and Kazakhstan.

Riassunto. Il Blocco del Karakorum è considerato una microplacca di origine Gondwaniana e fece parte del continente cimmerico (Mega Lhasa), che si staccò dal margine settentrionale del Gondwana durante il tardo Paleozoico. Viene descritta una fauna a coralli Rugosa dalla Formazione di Shogram nel Karakorum settentrionale (valli dello Yarkhun e Karambar), di età da Givetiano superiore a Frasniano inferiore. La fauna è dominata da generi cosmopoliti come *Hexagonaria*, *Disphyllum*, *Macgeea* e del gruppo *Temnophyllum/Spinophyllum*. In genere mostra una vasta distribuzione geografica, sebbene sia assente nel Reame dell'America orientale in tale intervallo di tempo. Di conseguenza i suoi componenti sono di scarso uso per ricostruzioni biogeografiche e per spiegare le relazioni tra il blocco Karakorum ed altri blocchi cimmerici. Una eccezione significativa é il genere *Pseudopexiphyllum* rinvenuto per la prima volta all'infuori della Turchia, indicando una connessione con la parte occidentale delle Cimmeridi.

A livello specifico, la fauna a coralli della Fm. Shogram è caratterizzata dallo sviluppo di una fauna differenziata e abbastanza unica con circa 35 taxa. Essi differiscono da faune ritenute coeve in blocchi crostali adiacenti. I legami faunistici con il microcontinente dell'Iran centrale (blocchi di Yazd e Tabas), con l'Elburz (NO Iran), il Pamir Centrale, il Blocco di Lhasa e il Qiangtang occidentale non sono chiari. Sebbene si ritenga che questi blocchi fossero adiacenti, forse non erano in contatto diretto durante il Devoniano. Tuttavia la fauna del Karakorum è significativamente vicina a quella del blocco di Helmand in Afghanistan, con una composizione generica molto simile e con specie morfologicamente connesse, anche se non identiche. Di conseguenza, il limitato scambio faunistico favorì lo sviluppo di nuovi taxa. La distribuzione delle nuove specie di *Spinophyllum*, *Pseudopexiphyllum* e *Pseudozaphrentis* é ristretta al Karakorum. Non sono chiari i motivi di

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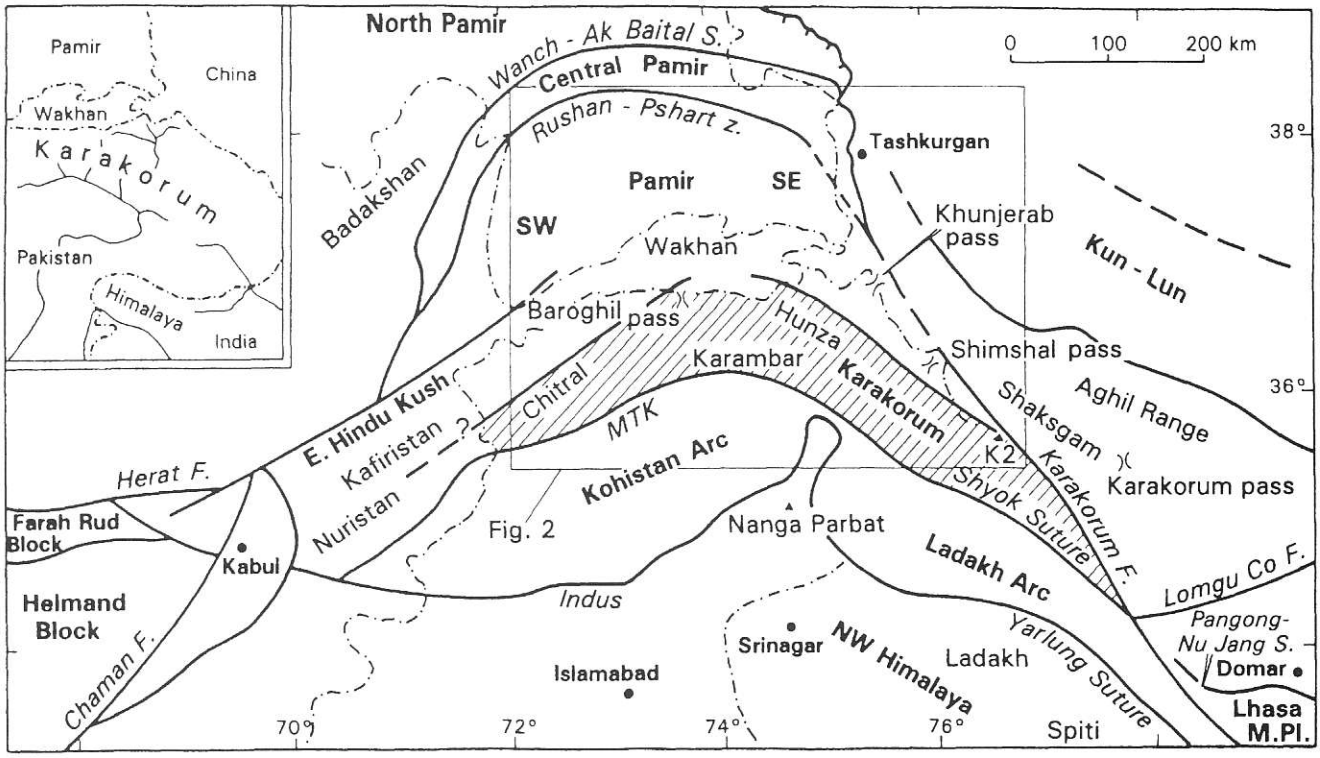

Fig. 1 - Tectonic units in the Karakorum (after Gaetani 1997a). Box shows outline of Fig. 2; hatched area marks are of northern sedimentary and southern metamorphic belt of Fig. 2.

questo sviluppo faunistico endemico e la scarsità degli scambi faunistici: forse fu attivo qualche tipo di barriera che condusse allo sviluppo di una fauna specifica per il Karakorum.

Con l'eccezione di *Phillipsastrea orientalis* Smith, 1930, conosciuta solo nel Devoniano della Birmania, il ritrovamento di alcune altre specie suggerisce l'esistenza di connessioni con regioni considerate non connesse biogeograficamente. Una debole relazione con le faune dell'Europa centrale è indicata dalla presenza di specie tipiche di *Macgeea e Hexagonaria*, conosciute nelle Ardenne e nelle Montagne della Santa Croce. Più insolite le affinità faunistiche con la regione dell'Altai-Sayan, indicate dalla presenza di specie di *Spinophyllum* e di siphonophrentidi, morfologicamente assai simili a quelli dell'Altai e del Kazakhstan.

Introduction and regional geology

Although Devonian sediments are widely distributed in the northern Karakorum Mountains (districts of Baroghil and Karambar), much of its geological structure and fossil content remained unknown for a long time. Coral faunas have never before been described from the area, but, where recorded, are from the geologically better known Chitral which is situated SW of the Karakorum. This area is thought to be structurally and paleogeographically closely related (Gaetani 1997, p. 341; Desio 1966, p. 311) and at least a few macrofaunistic investigations were carried out as part of regional iron-ore exploration (Calkins et al. 1981). The middle Givetian to Famennian Shogrâm Formation, which was introduced for a fossil-rich Devonian sequence in Chitral (Desio 1966, p. 296), is of major importance in this respect. Its sediments have been identified for more than 200 km along the "Northern Sedimentary Belt" from Chitral into the N Karakorum (Bender & Raza 1995; Gaetani et al. 1996, p. 693; Talent et al. 1999). This embraces also the collecting localities in the Yarkhun and Karambar Valley, which are extensions to the east of the Mastuj Valley. In this last valley lie the villages of Shogrâm, Reshun and Kurâgh in Chitral.

Comprehensive information on the geology and biostratigraphy of the northern Karakorum region was recently published by Gaetani et al. (1990, 1996) and Talent et al. (1999). Especially the regions of Baroghil and Karambar south of the Afghan Wakhan Corridor have been investigated and most of the stratigraphic age determination of the coral-yielding localities, which are discussed herein, are based on these works.

The Devonian rocks in the Upper Yarkhun and Karambar valleys crop out in different tectonic slices and units, both in the North Karakorum Sedimentary Belt (Gaetani 1997) which are interpreted to be remnants of the marginal area of the Karakorum Block. In the Baroghil and the Chillinji areas, a fairly continuous succession with well preserved fossils, including corals, is present. The Devonian successions starts with brown yellowish dolostones (Chilmarabad Formation) in beds 10-80 cm thick, with poorly preserved stromatoporoids and gastropods. Thickness ranges from 120 to 250 m.

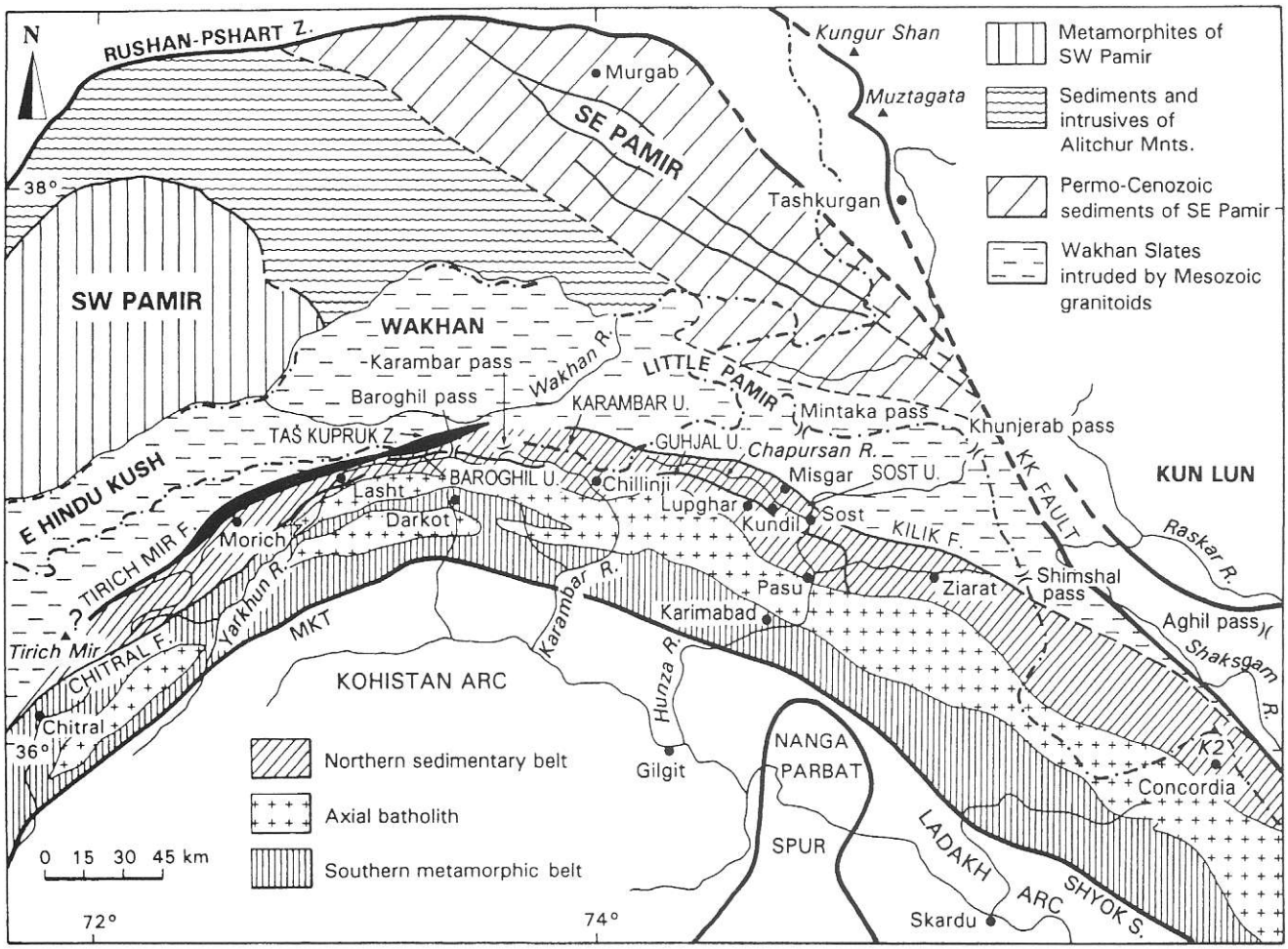

Fig. 2 - Geological structure in the Karakorum (from Gaetani 1997a). Abbreviations: MTK = "Main Karakorum Thrust", F = fault, U. = unit, R = river, S. = suture, Z = zone.

The Chilmarabad Formation is invariably overlaid by the Shogrâm Formation with an erosional surface. At the base microconglomerates or coarse quartzarenitic sandstone may form a continuous horizon, several m thick overlain by alternating fine sandstones, shales, calcareous sandstones and bafflestones. Brachiopods and bryozoans may be locally abundant. One or two bafflestone horizons are present in the middle upper part of the Shogrâm Formation spanning in age from Frasnian to Famennian, in which rugose and tabulate corals may be abundant. According to conodont data of Talent et al. (1999), there may be a lacuna within the Lower Frasnian succession. The bafflestone horizons may reach up to 10-15 m in thickness, and were recognised in four stratigraphic sections. According to the distribution of coral genera, which include no cystimorph corals, *Acanthophyllum*, *Grypophyllum* or other taxa which are more indicative of stratigraphic older intervals, the age of the fauna has to be regarded as Upper Givetian to Lower Frasnian. Determination of Famennian conodonts below the coral locality CK 377 in the Yarkhun River section by Talent et al. (1999, p. 212, fig. 4, locality CK 718) has to be questioned because of its typical upper Givetian/Frasnian coral fauna, which also proves the existence of a late Givetian to early Frasnian interval, not previously known from this section.

A record of *Spongophyllum* cf. *sedgwicki* from locality CK 1046 (Vandanil Formation), is much older than the majority of other specimens, and could be of Eifelian/Givetian age.

The discovery of Devonian rocks in the Chitral area can be traced back to the year 1899 when Major I.H. Grant sent some fossils collected in the Yarkhun Valley (Showar Shur) to the Geological Survey of India. Later on these fossils were described as a Lower Devonian fauna by Reed (1911, p. 86). Unfortunately the collecting localities of Grant have not been rediscovered and much of the Showar Shur area is composed of Permian rocks (Gaetani, pers. comm.). The first paper on Devonian fossils from Chitral (Reshun, Mastuj-Valley) was published by Hudleston (in McMahon & Hudleston 1902), describing several spiriferids and two species of "*Cyathophyllum*". First fossil lists of the so called "Shogram-Fauna" and a

comparison with contemporaneous European faunas were given by Hayden (1915), describing his observations on a walking tour along the rivers Mastuj and Yarkhun from Chitral (Shogrâm and Kurâgh in the Mastuj Valley) along the Karambar River to Baroghil into Hunza (via Darkot Pass) and the Pamirs (Fig. 2). Far ahead of his time, Hayden (1915, p. 277) was the first to discuss the possibility of a stratigraphical correlation between the Hindu Kush and Afghanistan, a question which has not lost its problematic nature up to the present day (Gaetani 1997a, p. 349; Shah 1977; Yazdi 2000).

Fundamental literature in the form of extensive monographs on Palaeozoic faunas, and in part still the most recent works on this subject, are without doubt the monumental works of F.R.C. Reed, who described numerous Palaeozoic faunas from the Himalaya, Kashmir and Chitral (Reed 1908, 1911, 1922). Some of those works are based on revisions of the fossils collected by Hudleston and Hayden. The most recent paper on Devonian corals from the Chitral has been presented by Schouppé (1965), but includes only a few taxa which are without much use for palaeogeographical as well as biostratigraphical questions. Moreover, Rugosa are only occasionally mentioned in a few faunal lists, as in Calkins et al. (1981), but most of these determinations are outdated and have to be questioned.

List of localities and determined rugose coral taxa:

Refer to Talent et al. (1999) for location and stratigraphic correlation of collecting localities.

CK473: Section Chillinji, level 6
Temnophyllum sp. MPUM 9096

CK644: isolated locality on the way to the Border Ridge section, NE of Lashkargaz, 4160 m
Siphonophrentis sp. A, MPUM 9097/1-2
Enallophrentis ? sp., MPUM 9098
Endophyllum sp., MPUM 9099/1-3
Spinophyllum sp., MPUM 9100
Keriophyllum sp., MPUM 9101/1-2
Stringophyllum acanthicum Frech 1885, MPUM 9148

CK657: Border Ridge Section, NE of Lashkargaz
Hexagonaria sp. C, MPUM 9102

CK658: Border Ridge Section, NE of Lashkargaz
Siphonophrentis sp. A, MPUM 9103
Siphonophrentis sp. B, MPUM 9104/1-2
Spinophyllum sp. cf. *varioseptatum* (Spasskiy, 1960), MPUM 9105/1-7.
Spinophyllum ? *shogramense* n.sp., MPUM 9106-9122
Macgeea cf. *gallica gigantea* Brice & Rohart, 1974, MPUM 9123/1-2
Phillipsastrea cf. *orientalis* SMITH 1930, MPUM 9124/1-3

CK 716 (= 371): Yarkhun River Section, SW of Gharil
Cyathophyllum afghanense (Brice, 1970), MPUM 9127/1-2

CK 377: Yarkhun River Section, SW of Gharil
Pseudopexiphyllum occultum n.sp., MPUM 9128-9130
Hexagonaria sp., MPUM 9131
Argutastrea sp. indet., MPUM 9149
Tryplasma ? sp. indet., MPUM 9132
Disphyllum cf. *caespitosum caespitosum* (Goldfuss, 1826), MPUM 9125
Disphyllum sp., MPUM 9126

CK 869: Siru Gol, SW of Lasht
Pseudozaphrentis sirius n.sp., MPUM 9133-9141
Macgeea ? sp., MPUM 9142/1-10
Macgeea cf. *multizonata* (Reed, 1922), MPUM 9143/1-9
Disphyllum caespitosum lazutkini (Ivanija, 1953), MPUM 9144/1-11
Hexagonaria cf. *sanctacrucensis* Moenke, 1954, MPUM 9145
Hexagonaria sp. B, MPUM 9146/1-2

CK 1046: Ribat Section, SW Karambar Pass, Vandanil Formation.
Spongophyllum cf. *sedgwicki* Milne-Edwards & Haime, 1851, MPUM 9147

Palaeogeographic implications of the coral fauna

It has generally been accepted that the biogeographical value of rugose coral faunas was decreasing during Devonian time. Beginning with highly endemic faunas during the Lower Devonian and maximum endemism during the Emsian, increasing faunal exchanges triggered by a continuous sea level rise in combination with "migrational events", led to the development of a cosmopolitan Upper Devonian faunal association (Oliver 1977; Pedder & Oliver 1990). Accordingly, the generic composition of stratigraphically young faunas is relatively uniform and Upper Givetian or Lower Frasnian benthic faunas are regarded as cosmopolitan, usually being characterized by *Hexagonaria*, *Disphyllum*, *Macgeea*, *Phillipsastrea* and characatophyllids. This explains the restricted value of Upper Devonian coral faunas for palaeogeographical reconstructions. Some minor, still prevailing differences in generic composition of otherwise closely related areas may be explained by the general rarity of some taxa. In addition, the recognition of faunal differences is in many cases limited by the material available for research. In this regard, the coral fauna of the Karakorum in Northern Pakistan is no exception to this rule and is dominated by cosmopolitan genera generally characterizing the Late Givetian to Early Frasnian. Still, provincialism can be recognized on species-level and contradicts the usual assumption of relatively shallow seas separating the isolated blocks of the Cimmerides during the Devonian. Wide seas, aside oceanic circulation patterns are most likely to have played important roles as faunal barriers (Fig. 3).

Desio (1966) defined the Shogrâm Formation with a typical occurrence of a calcareous-terrigenous succession at Shogrâm in Chitral. Later, Gaetani et al. correlated this succession with sections in the Upper Chitral region (Baroghil and Karambar districts) in the Northern Karakorum and accordingly both regions should be character-

ized by similar faunistic elements. However, the conodont faunas investigated by Talent et al. (1999) do not confirm such a close connection as they show only minor similarities with regions presumed to be palaeogeographically related. The coral faunas from the Hindu Kush and the Western Karakorum (Reed 1922; Schouppé 1965) are still insufficiently known, relatively poor in species and thus insufficient for a detailed comparison. Except for some widely distributed genera such as *Disphyllum*, *Macgeea* and *Phillipsastrea* there are no similarities on the species level. Most probably the fauna of Schouppé is slightly older than the one from N Pakistan which could explain its different composition. Desio (1966) however, was able to recognize a strong relationship between brachiopod faunas from Chitral and Afghanistan, reconfirmed by Angiolini et al. (1999) for Late Carboniferous brachiopods.

The compilation of Eurasian siphonophrentid corals by Pedder (1999) has shown that this group, previously endemic to the Eastern Americas Realm (EAR), had attained a very wide distribution during the Middle Devonian of the Old World. Therefore, the occurrence of such taxa in numerous central Asiatic coral faunas is only of minor use for biogeographical questions, especially as those forms are usually rare and adequate taxonomic treatment is almost impossible. Clearly more work has to be undertaken on this group of corals. The strong morphological similarities between the Karakorum siphonophrentids and those from the Altai-Sayan and Kazakhstan cannot be regarded as absolutely certain because of the low number of specimens available for investigation and would be unexpected, given the great distance between the two regions (Scotese 1990; Fig. 3). Because of strong morphological similarities to forms known from the Sauerland, aspects of homeomorphy should not be excluded. However, based on the distributional patterns of Lower Devonian Rugosa, Pedder & Oliver (1990, p. 270) and Pedder (1999, p. 391) support detachment of the Altai-Sayan from the Siberian Craton, placing it more to the south. *Spinophyllum* cf. *varioseptatum*, another Altai (Saur Mtns.) species recorded from the Karakorum, would support such a modification (Golonka 2002). The genus *Heliophyllum* Hall, a typical element of the EAR, has not yet been recorded from Central Asia.

Cyathophyllidae are generally rare in the fauna of the Shogrâm Formation, but the occurrence of *Cyathophyllum afghanense* indicates a connection to the reefal fauna of the Helmand Block in Afghanistan (Brice 1970). Generally, Afghan coral faunas are very similar and have almost identical generic composition, including the stratigraphically young siphonophrentids, but differ clearly in specific composition, indicating both regions were positioned rather close to each other but were not connected during the Devonian.

Disphyllum caespitosum lazutkini and *Macgeea multizonata* are widely distributed and common Frasnian species within Eurasia. Several species of *Hexagonaria* recorded from the Karakorum are remarkably similar to species known from the Holy Cross Mountains in Poland. *H. sanctacrucensis* as well as *H. mirabilis* are the most closely related species. In addition, there are similarities to the Afghan "*Prismatophyllum* cf. *magnum*". However, there are no connections with the numerous species of *Hexagonaria* known from the Ardennes, or to those recently described from the Pamirs (Schröder & Leleshus 2002) and Central Iran (Rohart 1999). This is rather surprising as the Central Pamir shows lithologic cycles rather similar to those observed on the Karakorum Block (Gaetani 1997, p. 349). A further hint to a European connection is given by *Macgeea gallica gigantea*, known only from the Frasnian of Ferques (N France) and the Ardennes. *Phillipsastrea* is recorded with only one species, very close to the Burmese *P. orientalis* from the Shan States (Padaukpin). The expected relation to *P. monticola* from Chitral Mountains cannot be confirmed because of insufficient description of this taxon.

Very surprising is the first record of a new species of *Pseudopexiphyllum*, as this genus was known only from the Early Frasnian of Turkey (Taurides). The Turkish coral faunas are insufficiently known; most of the existing literature is outdated and therefore of little use. Modern study is required based on new collections. Thoughts about palaeogeographic implications of the Turkish fauna are difficult to establish and it becomes very clear why Hubmann (1992) was complaining about our insufficient knowledge concerning the position Turkey held during the Devonian. Comparisons to neighbouring regions are almost impossible at this time.

New and reliable data on composition of rugose coral faunas of Central Iran have been given by Rohart (1999), but again the fauna does not show any striking relation to the one from the Shogrâm Formation. The palaeogeographical relations are directed more to the south and the west and many similarities may be found with faunas of Afghanistan, the Elburz Mountains, Turkey and Armenia, whereas other central Asian localities show only weak faunistic similarities (Brice et al. 1999). A corresponding low similarity becomes evident in comparing the Karakorum fauna to those from the possibly closely related Lhasa Block (Flügel 1966; Flügel & Tintori 1993). This is remarkable as the Western Qiangtang and especially the Lhasa Block are thought to be palaeogeographically related to the Karakorum, and most probably our limited knowledge on Tibetan rugose coral faunas is responsible for this gap. Following Yu & Liao (1982), Huang & Cheng (1988) described some stratigraphically older taxa from N Tibet, and it should be mentioned in this context that faunistic links to the Altai-Sayan area were again observed. A small Frasnian fauna from Rutong (NW Tibet) shows a cosmopolitic association of typical Upper Devonian taxa (Wu et al. 1982), that includes only one species - *Hexagonaria ngariensis* - that is very closely related and may be conspecific with *Hexagonaria* sp. D of the Yarkhun River section. A similar situation is evi-

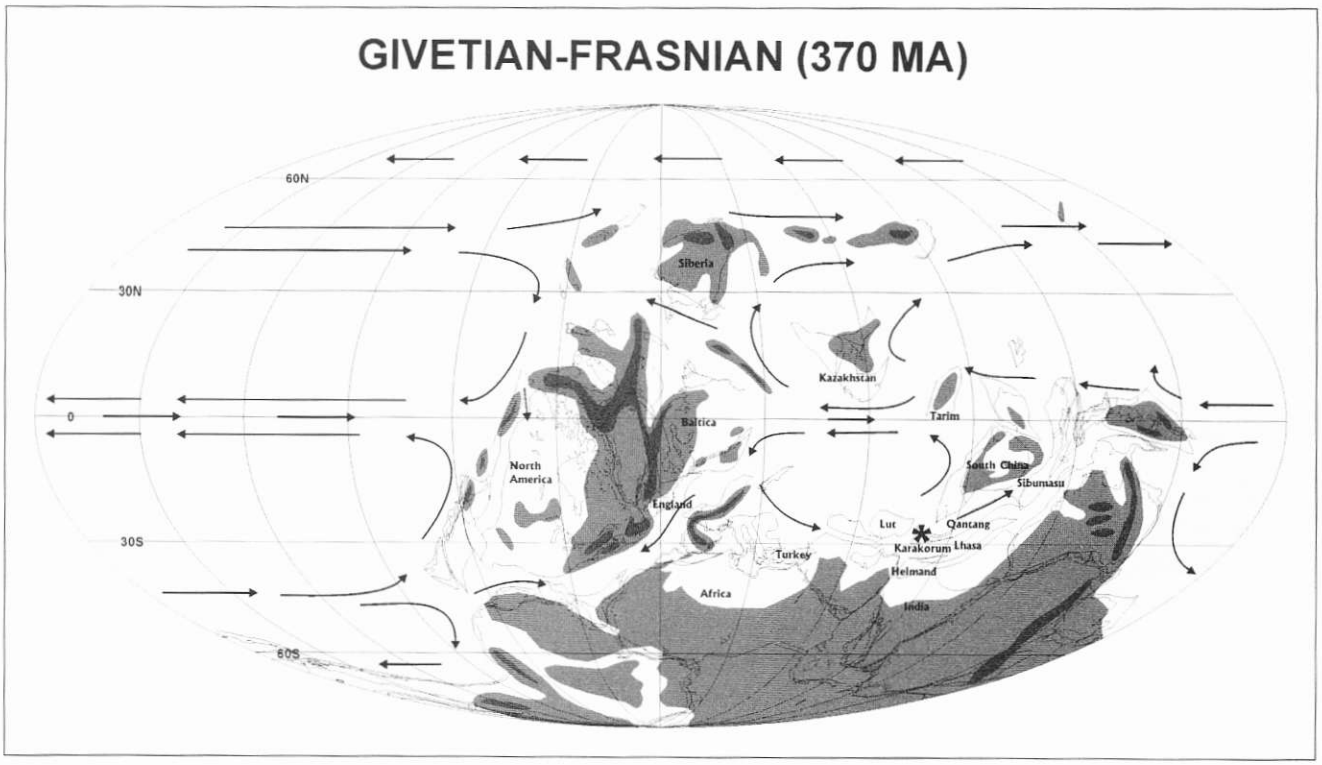

Fig. 3 - Reconstruction of Devonian palaeogeography and ocean currents (figure courtesy of W. Kiessling). [Dark grey areas: mountains; light grey areas: land areas]

dent when comparing the Karakorum fauna to the Upper Givetian one from Yunnan (Wang 1994). The Heyuanzhai Formation in Yunnan is dominated by *Macgeea*, siphonophrentids and *Neoacinophyllum* Wang 1994, and, apart from *Macgeea multizonata*, does not show any notable similarities with the Karakorum fauna. The faunistic relation to Western Australian fauna is also very weak. Two species of *Argutastrea* and *Disphyllum* show some resemblance to species known from the Canning Basin, but they differ too much to assign them to the same taxa. If the existence of an extensive isochronic reef belt along the northern margin of Gondwana (Yazdi 2000) can be proven and, more important, stratigraphically correlated, it seems that the species diversity on each of the Cimmerian terranes show specific differences in composition of their coral faunas, consistent with geographic isolation and restricted faunal exchange. This species provincialism has also been recognized by Talent et al. (1987) for Devonian and Lower Carboniferous brachiopod faunas which is consistent with lack of close proximity of the supposed Cimmerian crustal fragments postulated during the Devonian.

Systematic Palaeontology

The described material was collected by M. Gaetani during three expeditions to the Karakorum Mountains and is deposited in the Palaeontological Museum of the University of Milan, Italy, under the numbers MPUM 9096 to 9149.

Rugosa Milne-Edwards & Haime, 1850

Order **Cystiphyllida** Nicholson, 1889

Suborder **Pholidophyllina** Wedekind, 1927

Remarks. The similarities between the Silurian *Stauromatidium* Pedder & Oliver, 1982 and *Stringophyllum* Wedekind, 1922 are very obvious and the suggestion of Pedder (1999, p. 396) to include the Stringophyllidae in the Pholidophyllina - which are regarded as suborder of the Cystiphyllida - is more reasonable than to follow the interpretation of Hill (1981, p. F72) to include the genus within the Ptenophyllina Wedekind, 1927. The rather fine ptenophyllid septal structure differs strongly from stringophyllid septa which commonly break down into isolated, spine-like monacanthine trabeculae reminiscent of the septal morphology of tryplasmatid corals.

Stringophyllidae Wedekind, 1922

Stringophyllum Wedekind, 1922

Stringophyllum acanthicum Frech, 1885

(Pl. 4, fig. 5)

Material. One corallite MPUM 9148; locality CK644 on the way to the Border Ridge section, NE of Lashkargaz, 4160 m.

Remarks. With a diameter of 27 mm and 48 major septa the corallite is within the morphological variation observed in *S. acanthicum*, leaving little doubt that it is conspecific with that species. Septa consist of coarse monacanth trabeculae and are bisymmetrically arranged. Within the dissepimentarium they may be dilated by additional stereome and by additional thickenings on sections of dissepiments. Minor septa are commonly incomplete. The tabularium is about 15 mm wide and contains strongly concave tabulae typical for the genus. *S. acanthicum* is a common and widespread species in the Givetian of western Europe, but has also been recorded from the Tien-Shan (Frech 1911, p. 53, pl. 8, fig. 4) and SW China (He 1978, p. 152).

Order **Stauriida** Verrill, 1865

Suborder **Stauriina** Verrill, 1865

Siphonophrentidae Merriam, 1974

Siphonophrentis O'Connell, 1914

Type-species: *Caryophyllia gigantea* LeSueur, 1821.

Occurrence. The distributional data given by Pedder (1999) should be extended to include the Upper Givetian/Lower Frasnian of the Karakorum Range and the records mentioned in Schröder (2001) and Wrzołek (2002).

Siphonophrentis sp. A

Pl. 3, figs 4a, 5

Material. 3 corallites from the Border Ridge section; MPUM 9097/1-2, MPUM 9103.

Morphology. The few short, partly crushed and extensively eroded fragments of corallites are gerontic. No information is available concerning the taxonomically important early ontogenetic corallite development or the extent of the septotheca. The only characters that can be used for a determination are septal legth, their number, and development of septotheca and siphonofossula. Corallites have a large diameter of 4-6 cm and an accordingly high number of 56 major septa. In gerontic growth stages, amplexoid septa are rather short and reach about ⅓ to ½ of the radius. Minor septa are about half as long as the major ones. The cardinal septum may be shortened but does not lie within a clearly marked cardinal fossula. Generally septa are very thin to slightly dilated, so that a narrow, lamellar structured septotheca with a width of 1-2 mm is only occasionally developed at the outer wall. The only available longitudinal section shows an arrangement of axially flat or slightly concave tabulae, downturned at the outer wall, which is rather typical for the genus.

Remarks. In a detailed review of Old World *Siphonophrentis*, Pedder (1999) assigned numerous Eurasian/northern African taxa to *Siphonophrentis belgebaschica* Ivaniya, 1955. It is difficult to answer if the inclusion of geographically sometimes widely separated occurrences and/or species is appropriate. The simple morphology and insufficiently documented variability of most of these taxa makes this question difficult. There are only a few, often highly variable diagnostic characters which may be used for a morphological separation of species and our understanding of numerous species is still fragmentary as populations are usually not available for study. Even more difficult is the identification and interpretation of numerous records described under open nomenclature.

The specimens from the Border Ridge Section are not assigned to *S. belgebaschica*, as their major septa are shorter and only weakly dilated so that thickenings are restricted almost completely to the septotheca. One section of *Zmeinogorskia bublichenkoi* Spasskiy, 1960 from the Eifelian of the Rudny Altay (see Pedder 1999, p. 400) has very similar developed thin, axially bent septa (Spasskiy 1960, pl. 12, fig. 1), but other specimens assigned by Spasskiy to the same species differ in having strongly dilated septa (Spasskiy 1960, pl. 11, fig. 3; pl. 13, fig. 1). Almost identical, indeed inseparable from the Border Ridge material, is one transverse section of a corallite with comparably thin septa of "*Siphonophrentis* ? sp." collected from the Upper Givetian Iserlohn Group of the Eastern Rheinisches Schiefergebirge (Sauerland) figured by Schröder (2001, fig. 1.6). The frequently mentioned and common Spanish species *S. cantabrica* Birenheide, 1978 differs generally in having a lower number of septa and a smaller diameter.

Siphonophrentis sp. B

Pl. 4, figs 3a, b

Material. 2 corallites from the Border Ridge Section, MPUM 9104/1-2.

Remarks. Both fragments of corallites differ from *Siphonophrentis* sp. A by their much smaller diameter of 20 and 25 mm respectively and lower number of 40 major septa. They might prove to be juvenile corallites of *Siphonophrentis* sp. A, but the slightly longer major septa, comparably short minor septa and the more strongly reduced cardinal septum warrant separation until more information is available on variability.

Superficially both specimens show some similarities to the small *Siphonophrentis minor* Sung, 1982 described by Wang (1994) from the Upper Givetian Heyuanzhai Formation of Yunnan. However, the Chinese samples do not show a clearly developed fossula, and have a wide stereozone, which makes an assignment to *Siphonophrentis* questionable. Pedder (1999, p. 399) suggested these specimens should probably be included in *Baoshanophyllum* Song, 1974.

Enallophrentis Oliver, 1994

Type-species: *Strombodes simplex* Hall, 1843.

Occurrence. Lower and Middle Devonian of the Eastern Americas Realm; Middle Devonian of Northern Africa and Eurasia.

Enallophrentis ? sp.

Pl. 3, fig. 4b; Pl. 4, fig. 4

Material. 1 corallite MPUM 9098; locality CK644 on the way to the Border Ridge section, NE of Lashkargaz, 4160 m.

Morphology. One weathered corallite with a diameter of 45 mm and peripherally strongly thickened septa forming a broad septal stereozone 3-5 mm thick. Within this wide stereozone, peripheral parts of septa are only poorly preserved and may become indistinct. Septal insertions at the epitheca are no longer visible as their microstructure is changed completely to a lamellar structure and there are no clear traces of trabeculae. The strongly amplexoid major septa number 48 and may reach almost to the axis. A cardinal fossula is only indicated by the arrangement of tabulae in transverse section, which is incomplete in its cardinal quadrant. Minor septa are remarkably long and completely traverse the wide peripheral septal stereozone. In longitudinal section, the closely spaced tabulae are complete and slightly convex, downturned at their periphery.

Remarks. Available information on the corallite suggests assignment to the siphonophrentid *Enallophrentis*. However, as septal microstructure and ontogenetic development is unknown, the specimen is only tentatively assigned to this genus; comparison with possibly related taxa is difficult.

There are two species which show some similarities. Similar sized *Zmeinogorskia zaisanica* Spasskiy, 1960 from the Givetian of the Saur Range (E Kazakhstan), has a comparable septal number, long septa of both orders, and a wide septotheca (Spasskiy 1960, p. 121, pl. 4, fig. 1). Persistence of its axial vortex cannot be estimated, but is generally known to be a highly variable character, at least in *E. rhenana* Schröder et al., 1996. This Upper Eifelian species from the Eifel differs by its much narrower stereozone.

Suborder **Ketophyllina** Zhavoronkova, 1972

Endophyllidae Torley, 1933

Within the colonial Endophyllidae, the genera *Sanidophyllum* Etheridge, 1899 and *Blysmatophyllum* Pedder, 1970 are distinguished from *Endophyllum* mainly because of their distinctive phaceloid-subcerioid growth form. In these genera cerioid growth is induced by contacts of lateral calical expansions in generally phaceloid arranged corallites. Although specimens described here show a phaceloid-subcerioid growth form, in which they differ from typically developed cerioid *Endophyllum*, they are assigned here to that genus.

In any case, there are striking resemblance concerning the lateral calicular expansions of corallites embedded in sediment which are similarly developed in the Australian species *B. isisense* Pedder, 1970 or *B. multigemme* Zhen, 1994 (Zhen 1994, fig. 5). However, as there are only a few fragments available, it cannot be excluded that they belong to a species of *Endophyllum* which is only periodically developing a phaceloid growth, or young corallites positioned close to the colony surface. Jones (1929, p. 85) remarked that growth form in *Endophyllum* may also vary considerably within the same colony, ranging from sub-phaceloid to cerioid. Closely cerioid growth stages of *Blysmatophyllum* species are very similar to species of *Endophyllum* Milne-Edwards & Haime, 1851. Accordingly, classification of such "transitional" species like "*Blysmatophyllum* ? sp." from the Givetian of Queensland (Zhen 1994, p. 315) proves to be very difficult.

Endophyllum Milne-Edwards & Haime, 1851

Type-species: *Endophyllum bowerbanki* Milne-Edwards & Haime, 1851.

Occurrence. Lower Devonian of Eastern Australia and Central Asia, widely distributed in the Old World Realm in the Middle and Upper Devonian (Frasnian), except for western North America and the Eastern Americas Realm.

Endophyllum sp.

Pl. 4, fig. 6; Pl. 5, figs 3-4.

Material. 3 fragments of colonies, MPUM 9099/1-3. Locality CK644 on the way to the Border Ridge section, NE of Lashkargaz, 4160 m.

Description. Colony size is not known and fragments consist of a few mostly incomplete corallites reaching a diameter of approximately 2-3 cm. Corallites are closely spaced but not in contact with each other at all places and growth form has to be regarded as phaceloid to subcerioid. Isolated corallites are predominantly circular shaped and are only in lateral contact with each other where the dissepimentarium is extending outwards, producing calicular expansions. Accordingly, remaining spaces between corallites are infilled by sediment (Pl. 4, fig. 6). In peripheral parts of some cross-sections between corallite margin and tabularium boundary there may also be sediment deposits, replacing the wide zone of common lonsdaleoid dissepiments, which are developed as large and irregular shaped presepiments, interrupting the septa. Some septa may be reduced to short spines inserting on presepiments close to the periphery of corallites. Coral-

lite walls and septa are generally thin. Major septa number approximately 30 and reach, or nearly reach the axis, leaving a small space free. Minor septa are much shorter and may be reduced to spines on the lonsdaleoid dissepiments. Generally septa are thin. Occasionally they may be slightly wavy and vepreculate in their peripheral parts, whereas axial parts are sometimes ornamented with short flanges. Tabularium diameter ranges between 10-13 mm. It is composed of concave or flat tabellae and an inner zone of flat tabulae with downturned edges. Dissepimentarium is wide and contains a few rows of mainly large, elongated and steeply inclined presepiments with thickened walls.

Remarks. *Endophyllum* is generally a widely distributed genus in Eurasia and its species were recorded from numerous Middle Devonian localities in Europe (Spain, Germany, England) and Asia (Kuznetsk Basin, Kazakhstan, several from China, Afghanistan). Some of those were assigned to *E. abditum*, but in most cases their specific identity is difficult to ascertain (Oliver et al. 1996, p. 54).

It is impossible to estimate the development of subcerioid to phaceloid corallites in the material collected on the way to Border Ridge section, but several known species show similar morphology, for example *Endophyllum yunnanense* Mansuy, 1912 from the Middle Devonian of Po-Shi (Yunnan). Corallites of such colonies are typically cerioid, but some may become phaceloid and have a rounded outline (Fontaine 1966, p. 71). As the material consists only of a few incomplete fragments of mostly isolated corallites, giving no reliable data on its growth form or biometrical data, it does not allow specific determination.

Suborder **Cyathophyllina** Nicholson, 1889

Cyathophyllidae Dana, 1846

Cyathophyllum Goldfuss, 1826

Type-species: *Cyathophyllum dianthus* Goldfuss, 1826.

Occurrence. Widely distributed in the Middle Devonian of Europe and Australasia.

Cyathophyllum afghanense (Brice, 1970)

Pl. 3, fig. 2

Holotype, locus typicus and stratum typicum. See Brice 1970, p. 269.

Material. 2 fragments of colonies, MPUM 9127/1-2. Yarkhun River Section, SW of Gharil.

Description. Available colonies reach a maximum diameter of approximately 10 cm and consist of only a few large and cerioid arranged corallites. Corallite diameter in adult stage measures about 5 cm and mode of increase is lateral as well as peripheral parricidal. In one colony all corallites are affected by simultaneously offsetting numerous daughter corallites, completely disrupting their mother corallites. In corallites unaffected by parricidal increase, there is a wide, slightly inclined calicular platform, and the calice is slightly funnel shaped. Generally septa are very slender and are not affected by any skeletal thickenings or sclerenchymal coatings. In adult stage, number of major septa is about 36. They extend to the corallite axis whereas minor septa are only slightly shorter, terminating at the tabularium boundary. The cardinal septum is not differentiated. All septa are complete and usually strongly carinate. Short zigzag carinae are the most common type, but a few carinae of the yardarm type may also be developed. Tabularium is narrow (5-7 mm) and contains numerous small tabellae in a generally convex orientation. The very wide dissepimentarium is composed of numerous small globose dissepiments, steeply inwardly inclined close to the tabularium boundary but showing layers of flat or slightly convex oriented dissepiments in its outer parts. Sections of carinae are frequently traversing the dissepimentarium.

Remarks. *Cyathophyllum afghanense* from the Givetian of Afghanistan (Helmand Block) corresponds very well to the specimens from the Karakorum. Compared to the material from Dacht-e-Nawar there are only minor differences in corallite-size and septal development (Brice and 1970, p. 269, pl. 19, fig. 7) and the colonies are most certainly conspecific. This species is very closely related to *Cyathophyllum planum* (Ludwig, 1866) from the Eifelian of the Eifel and probably has to be regarded as a younger subspecies. *Cyathophyllum multicarinatum* Coen-Aubert, 1989 from the Eifelian of the Ardennes differs in having a less numerous number of septa and more strongly developed coarser carinae. *Peripaedium gigantium* Aung, 1995 (Eifelian of the Shan States, Myanmar) is most probably a synonym of that species.

Keriophyllum Wedekind, 1923

Type-species: *Keriophyllum heiligensteini* Wedekind, 1923.

Keriophyllum sp.

Pl. 7, fig. 1

Material. 2 corallites, MPUM 9101/1-2, locality CK644, on the way to the Border Ridge section, NE of Lashkargaz, 4160 m.

Morphology. Corallites reach a diameter of about 20 mm and a length of more than 40 mm. The thin epitheca is only partly preserved and is not dilated by peripheral septal bases. Septa are very thin and undulated but always carinate. The development of carinae varies considerably in both specimens and there are sections with heavily carinated septa as well as almost smooth septa. Irregular carinae of the zigzag type predominate, but some isolated yardarm carinae may be observed. There are 29 major septa, reaching to or almost to the corallite axis, where they leave a small axial space and may be slightly

twisted. Minor septa are 2/3 to 3/4 as long as the radius and do not extend far into the tabularium, which has a diameter of 7-8 mm. The dissepimentarium consists of numerous rows of small globose dissepiments arranged according to a weakly funnel-shaped calice.

Remarks. The rather strong carinate septa relate this relatively small species to the stratigraphically older forms of the genus. A similar septal morphology with strongly carinate septa that may disintegrate into isolated trabeculae and become retiform at their ends is particularly well known in taxa from the lower Middle Devonian of the Eifel. In this regard *K. cylindricum* (Schulz, 1883) is a closely related species, but the Eifel species has a larger diameter and a higher number of septa. Birenheide (1968) regards this taxon as a synonym of *K. turbinatum* (Goldfuss, 1826).

The stratigraphically youngest records of *K. cylindricum* from possible Givetian strata of Dacht-e-Nawar W of Ghazni in Afghanistan (Brice, 1970, p. 267, pl. 18, fig. 4) and those from the Upper Devonian of the Kurâgh Spur (Reed 1922, pl. 1, fig. 5) suggest that similar but slightly younger forms are widely distributed in Central Asia. However, these records are imperfectly known and it is questionable if they are indeed conspecific with the European species. Detailed comparison is difficult from available descriptions and figures.

Several species of *Keriophyllum* from the Upper Eifelian or Givetian closely resemble the specimens from the Karakorum as regards size and septal number. Typical examples for such small diameter species are *Cyathophyllum postarduum* Birenheide & Soto, 1992 known from the Upper Givetian of northern Spain or the Lower Givetian *Keriophyllum maillieuxi* (Tsien, 1966) from the Ardennes, but both can be distinguished by their less strongly carinate septa.

Suborder **Columnariina** Soshkina, 1941
Family Charactophyllidae Pedder, 1982

Spinophyllum Wedekind, 1922
Type-species: *Campophyllum spongiosum* Schlüter, 1889

Remarks. Species of the *Spinophyllum/Temnophyllum* group are known to vary considerably in their septal morphology; without a detailed description of their variability it is very difficult to assign them properly. This led to the introduction of numerous new species and lengthy discussions of their generic identity as well as erection of new genera sich as *Truncicarinulum* Yu & Kuang, 1983 or *Paracanthus* Merriam, 1974 to accomodate such intermediate taxa.

The wide variation in septal morphology makes it indeed difficult to assign the specimens with certainty to already described species or even to a genus. In addition, descriptions of many already known species are insufficient; revisions are needed for most of these taxa. A thorough study of variability has been undertaken for only a few Eurasian species which were subsequently well illustrated by more extensive series of thin sections, for example the type species of *Spinophyllum*; *Spinophyllum spongiosum* (Schlüter, 1889) by Birenheide & Lütte (1990), *Spinophyllum liujingense* (Yu & Kuang, 1984) and *Spinophyllum blacourti* (Rohart, 1988) by Coen-Aubert (2002).

Spinophyllum cf. **varioseptatum** (Spasskiy, 1960)
Pl. 2, figs 2-6; Pl. 9, fig. 8

Holotype, locus typicus, stratum typicum and diagnosis. See Spasskiy 1960, p. 126.

Material. 7 corallites, MPUM 9105/1-7, CK658, Border Ridge Section, NE of Lashkargaz.

Description. Small, trochoid to subcylindrical corallites with a diameter of 14-21 mm at a maximum length of 32 mm. In cross-section, septa are strongly carinate; occasionally the very stout and regular arranged carinae may be thickend by additional stereome (Pl. 9, fig. 8). In such corallites carinae may touch with those of neighbouring septa. The strongest septal thickenings are developed at the periphery of the tabularium and the axial tips of septa which are sometimes spear-shaped close to the morphology developed in *Charisphyllum* (see Oliver & Sorauf 1988). Contrasting with this, in some corallites septa are only slightly thickened and weakly carinate. The number of major septa ranges from 26 to 31. They are only slightly longer than the minors and extend through about 2/3 of the radius, so that they leave a small open area at the corallite axis with a diameter of 5 to 8 mm. The cardinal septum may be strongly shortened. The most conspicuous character of the longitudinal sections are the comb-like, upwards and inward oriented structures of yardarm carinae, frequently traversing the dissepimentarium. The dissepimentarium is rather narrow and consists of only a few rows of small dissepiments. Close to the tabularium boundary they are very similar to periaxial tabellae and consequently the boundary to the tabularium appears not very sharp. Tabulae are only complete in the central part of the tabularium, where they are commonly arranged as horizontally or slightly convex oriented plates. Although the generally short septa of this species may not disrupt the tabulae, the tabularium consists mostly of small tabellae and its diameter measures about 7 to 11 mm.

Remarks. Corallites are closely comparable with *Spinophyllum varioseptatum* from the Upper Givetian of the Saisan Formation of the Saur Mtns. (Altai, Churchy Sai River). The holotype of this species (Spasskiy 1960, pl. 7, figs 2a-b) has a slightly higher number of septa, but shows similar short septa, not extending to the corallite axis, leaving a small space at centre and a tabularium composed predominantly of tabellae. In regard to the variable development of the irregularly dilated carinae, there are also strong similarities between both species. The assignment

of the paratypes figured in Spasskiy (1960, pl. 7, figs 1a-b) to *S. varioseptatum* is questionable, as both transverse sections have smooth septa with spindle-shaped dilations (see Dubatolov & Spasskiy 1971, p. 102, figs 2a-b). The species referred to *Heliophyllum* by Bulvanker (1958, p. 104) and which are discussed by Spasskiy belong - with the exception of "*Heliophyllum* ? *originale* Bulvanker", which has strongly dilated septa - to *Cyathophyllum* sensu lato.

Some corallites with uniformly developed yardarm carinae show a remarkable close resemblance to some species of *Spinophyllum* known from the Cantabrian coast of Asturias (Spain). Those Upper Givetian populations are currently assigned to *Spinophyllum altevogti* (Oliver & Sorauf, 1988), but the material is very heterogenous in regard to septal dilation as well as carinae development and may be split up into more than one species. Apart from the populations illustrated by Oliver & Sorauf (1988, fig. 5-6), with sometimes extremely thickened septa (Oliver & Sorauf 1988, fig. 6A), there are phenotypes which differ in having only weakly dilated, but strongly carinate septa and which are almost indistinguishable from the Karakorum corallites.

Spinophyllum? shogramense n. sp.

Pl. 2 fig. 7-10, Pl. 3 fig. 3, Pl. 7 fig. 8-9.

Holotype. MPUM9106

Locus typicus. N Pakistan, Upper Karambar River, N Laskargaz, Border Ridge Section, horizon CK 658 (compare Talent et al. 1999, fig. 3-4).

Stratum typicum. Devonian, Shogrâm Formation, middle Givetian to Frasnian.

Diagnosis. *Spinophyllum* ? with corallites of 18-23 mm in diameter. Septa highly variable thickened and carinate, numbering 32-39 of each order. Major septa withdrawn from axis, minors reaching 2/3 to 3/4 of the radius. Tabularium wide, about 10 mm in diamter.

Paratypes. 16 corallites, MPUM 9106-9122.

Description. Fragments of solitary corallites are short, ceratoid to subcylindrical. Diameter ranges in most specimens between 18 and 23 mm, but rarely may reach 27 or 30 mm. Although they are strongly weathered and corallite walls are generally only poorly preserved, some wedge-like septal thickenings are still present at the peripheral parts of septa in transverse sections. In most sections septa are thin to slightly dilated but they may be strongly thickened in some. They are thickest in their middle part, with a maximum dilation within the inner dissepimentarium, but they are never contiguous laterally and a stereozone is not developed. Septa are predominantly smooth, some with knot-like lateral expansions or more rarely weakly carinate with irregularly developed thickened carinae at peripheral parts, occasionally approaching the morphology of the *Spinophyllum*-type (Pl. 2, fig. 9). However, even within the same transverse section, thickening of septa varies considerably so that there may be very thin, smooth septa and dilated, weakly carinate septa within the same corallite. There are 32-39 major septa which are attenuate within the tabularium and withdrawn from the axis (about 2/3 to 3/4 as long as the radius), so that a small septal free space with a diameter of 2-6 mm remains free. Tabularium is well defined in transverse section by major septa, abruptly thinning on their entry into the tabularium, as well as by short minor septa, just extending into the tabularium. Its diameter (calculated from transverse sections by the axial space free of minor septa) measures about 10 mm. In longitudinal section its central part contains flat or slightly convex axial tabellae with downturned edges and adaxially inclined peripheral tabellae, so that there is no sharp boundary to the dissepimentarium. The dissepimentarium consists of numerous rows of small globose and steeply inclined dissepiments, which are oriented according to a funnel-shaped calice.

Remarks. This species is morphologically intermediate between *Spinophyllum* and *Temnophyllum* as septal thickening and carinae development are highly variable characters within the population as well as in single corallites. Septa may be weakly thickend and smooth or dilated and carinate even within one transverse section (Pl. 2, fig. 9). However, in the majority of specimens, septa are generally weakly dilated and very faintly carinate. None of the corallites displays a stereozone of thickened septa or consistently developed *Spinophyllum*-like carinae and is thus only tentatively assigned to *Spinophyllum*.

Sinodisphyllum sp. from the Shishtu Formation of Tabas/E Iran (Rohart 1999, p. 58, pl. 9, fig. 3-4, pl. 10, fig. 5) has likewise weakly carinate, but spindle-shaped septa that reach to the corallite axis where they are commonly twisted to a vortex. The species is closely related but differs from the Karakorum samples in having a larger corallite diameter and longer septa. Typical *Sinodisphyllum* is characterized by generally thin and smooth septa lacking carinae or lateral projections (McLean 1994, p. 113) and is morphologically close to *Glossophyllum*.

Especially from the Devonian of South China, numerous species described in the last decades have to be considered in comparison with the specimens from the Karakorum. However, most of those taxa were insufficiently documented and do not allow detailed comparison. Several species known from the Middle Devonian of Yunnan (Wang 1948) resemble *Spinophyllum* ? *shogramense* in many respects. Closely related are *T.* (*Temnocarinia*) *complicata* (Wang, 1948) and *Cyathophyllum expansum* Wang, 1948. They also belong to a species-group with rather thin to slightly dilated and faintly carinate septa without development of a stereozone, but are distinguished from *S.* ? *shogramense* by their stronger carinate, axially thickened septa. *Keriophyllum heiligensteini* Wedekind *sensu* Wang 1948 (pl. 2, fig. 8-11) is characterized by thin septa which are weakly carinate/serrate and should be placed within the *Spinophyllum*/*Temnophyllum*-group. It is difficult to consider the variability of the species described by Wang (1948) from the figures given, but most probably some species have to be synonymized.

Spinophyllum zhongguoense (He, 1978) from the Givetian of Sichuan differs in having stronger developed yardarm carinae and longer septa reaching to the corallite axis. More closely related is a corallite from the Givetian of Dushan (Guizhou) which has been referred to *S. zhongguoense* (Birenheide & Liao 1985, p. 245, pl. 2, fig. 9). It has weakly dilated septa not reaching to the corallite axis, but differs in its lower number of septa. The corallite figured by Liao & Birenheide (1989, pl. 2, fig. 12) as *Spinophyllum hejiazhaiense* (Kong, 1978) has a remarkably wide dissepimentarium and is most likely conspecific with *S. zhongguoense*. "*Temnophyllum* (*Truncicarinulum*) *heterophylloides*" *sensu* Kong in Kong & Huang (1978, p. 100, pl. 33, fig. 4) *non* Frech, 1885 is distinguished by its longer, spindle-shaped septa while *Charactophyllum posterum* Ivaniya, 1965 can be separated by its larger diameter and higher number of septa.

Pseudozaphrentis Sun, 1958

Type-species: *P. difficile* Sun, 1958.

Remarks. During the last decade several authors have discussed the taxonomic content and validity of this genus (Liao 1977; Lütte 1990; McLean 1994, p. 111; Coen-Aubert 1995, p. 164; Zhen & Jell 1996, p. 79, Schröder & Salerno 2001, p. 118, Coen-Aubert 2003). Apart from accepting it as a valid and independent genus, generic identity with *Temnophyllum* or *Charactophyllum* was discussed (Pedder 1972; McLean 1994), but this proposed synonymy has been accepted only reluctantly.

Variability of the type-species *P. difficile* from the Upper Frasnian of Xiang Xiang, Hunan (Shetienchao Fm.) is still insufficiently known. As far as can be estimated from the original figures of Sun (1958, pl. 7, fig. 4), the dilation of axial septal ends in the type species varies considerably but normal (concave) sections of dissepiments with a slight tendency to become arranged in a herringbone pattern dominate. Lateral dissepiments or presepiments are rare. However, new collections from Hunan and Guangxi proved the existence of charactophylloid trabeculae (Coen-Aubert 1995, pl. 1, fig. 7-10). *Pseudozaphrentis* has been widely used to accomodate Chinese species (Liao 1977), but during the last years non-Chinese taxa have been included; the genus was recently treated as a subgenus of *Temnophyllum* by Zhen & Jell (1996).

The morphology of numerous species with shortened minor septa, weak to moderate septal dilation and herringbone dissepiments suggest assignment to *Pseudozaphrentis*, and the reduction of minor septa in this group seems to follow a phylogenetic trend. The group is distributed worldwide and is characteristic of many coral faunas of Givetian to Frasnian age. Usually they have been assigned to *Mictophyllum*, *Sinodisphyllum*, *Temnophyllum* or - following the Russian terminology - to *Neostringophyllm* or *Aulacophyllum*. *Mictophyllum* Lang & Smith, 1939 has recently been placed within the Kyphophyllidae (McLean 1994) and *Sinodisphyllum* is a genus with typically thin septa that is close to *Aristophyllum*. This group differs strongly from *Temnophyllum* in having reduced minor septa and weak septal dilation, which is never enough to form a wide stereozone, but is restricted to the inner dissepimentarium. *Chostophyllum* is a very closely related genus that differs in having generally short septa of both orders, a more clearly marked cardinal septum and almost no herring-bone dissepiments. *Aristophyllum* Bul'vanker, Spasskiy & Kravtsov, 1975 is morphologically intermediate between *Chostophyllum* and *Pseudozaphrentis*.

The numerous Devonian examples which were not originally assigned to *Pseudozaphrentis* include - among others - the following Givetian species: *Sinodisphyllum* of Kong & Huang 1978, Guizhou; *Mictophyllum* of Lütte 1990, Eifel Hills; *Mictophyllum schlueteri* Birenheide & Lütte, 1990, pl. 4, figs 26-27, Eifel Hills; *Mictophyllum* of Liao 1977, Guizhou; *Temnophyllum lenzi* Pedder, 1972 and *T. richardsoni* (Meek, 1868) of Pedder 1972; McLean, (1993, fig. 1.5), North West Territories; *Temnophyllum zamkowae* Wrzołek, 1992, Holy Cross Mtns.; or Frasnian species: *Mictophyllum* of He 1978, Sichuan; *Mictophyllum guniae* Różkowska, 1979, Sudetes; *Neostringophyllum modicum* (Smith, 1945) of Soshkina 1951, Ural; *Aulacophyllum pepelaievi* Bul'vanker, 1965, NE Siberia; the holotype of *Aristophyllum simakovi* Bul'vanker, Spasskiy & Kravtsov, 1975, Kolyma River Basin; *Piceaphyllum* sp. cf. *Temnophyllum menyouense* (Hill & Jell, 1970) of Wright et al. (1990, fig. 17), New South Wales.

The type-series of *Mictophyllum modicum* Smith, 1945 from the Frasnian of the Mackenzie River Region, Canada, is characterized by even more reduced minor septa and the occurrence of lateral as well as lonsdaleoid dissepiments. It has been suggested by McLean (1993) that it is morphologically close to, although not typical for *Piceaphyllum* Różkowska 1979. *Neotemnophyllum* Yu & Kuang, 1984 and *Fruehwirtia* Flügel, 1993 from the early Frasnian of Nepal are synonyms of this genus.

Only one species of Smith (1945, pl. 5 fig. 3) with rather strong septal dilation is rather close to the definition of *Piceaphyllum* and its type species *N. pronini* Soshkina, 1951. In addition, septa may bear carinae like projections, split peripherally into numerous lateral dissepiments infilling the interseptal loculi and there are no traces of presepiments. Minor septa may be reduced in juvenile sections but are long in the gerontic stage (Soshkina 1951, p. 61, pl. 10; 1954: pl. 26, fig. 89). Most probably *M. modicum* is a very progressive phenotype of the *Pseudozaphrentis* lineage characterized by continuous degeneration of minor septa which may be replaced by presepiments.

Pseudozaphrentis sirius n. sp.

Pl. 7 figs 2-7

Holotype. MPUM 9133.

Locus typicus. Siru Gol, approximately 8 km W of Sakirmul village. (Talent et al. 1999, fig. 1; locality 2)

Stratum typicum. Devonian, Upper Givetian?, Shogrâm-Formation.

Derivatio nominis. After the star.

Paratypes. 8 specimens, MPUM 9134-9141

Diagnosis. A species of *Pseudozaphrentis* with a corallite diameter ranging from 20-23 mm and 24-28 major septa, which do not reach the corallite axis. Septa thin to moderately dilated. Minor septa commonly reduced and replaced by herringbone dissepiments. Rare presepiments may interrupt the septa.

Description. Fragments of corallites reach a maximum diameter of 20-23 mm at a length of 2-3 cm. Juvenile corallites are trochoid, but become subcylindrical in adult stage and have funnel-shaped calices with moderate to steeply inclined calice walls.

Septal length is highly variable, and there is no general trend even in early ontogenetic stages. Usually a small axial space of 1-2 mm in diameter remains, increasing strongly in adult corallites. Generally septa are inserted at the corallite wall, but some may be interrupted by rare presepiments (Pl. 7, fig. 2b). Septal bases are thin to slightly wedge-shaped and dilated, and especially in juvenile specimens a weak stereozone may be developed. Additionally, outer walls of the innermost row of dissepiments may be thickened, so that a weak "inner wall" may occasionally be present at the boundary of the tabularium. In places the stereome coating the dissepiments is spread to the septa which are then slightly dilated. Major septa are short, reaching about 1/2 to 2/3 of the radius and in most sections they are not much longer than the minor septa which reach about 1/4 to 1/2 of the radius if well developed. However, minor septa are commonly incomplete or completely reduced and replaced by herring-bone dissepiments.

Number of major septa ranges from 24 to 28. In adult corallites short major septa become thread-like and are slightly twisted. Interseptal elements are steeply inclined but there are no lateral dissepiments. Longitudinal sections are characterized by the unusually wide tabularium with predominantly complete tabulae, horizontal or weakly convex and sometimes supplemented by a few sporadic large tabellae. Dissepimentarium is very narrow and consists of only one row of small elongate dissepiments in juvenile sections and up to 5 rows in adult stage. Because of the short and sometimes very thin septa, the nature of trabeculae is difficult to observe, but some sections suggest a rather horizontal arrangement.

Remarks. Charactophyllidae are a widely distributed coral family, especially common and diverse in Givetian and Frasnian faunas. Because of their high intraspecific variability the taxonomic status of many of the described species remains unclear and specific separation of closely related taxa is not without problems. In addition, the majority of the known taxa are still insufficiently documented and thorough revisions, which should include studies on intraspecific variation, are needed for most species. Consequently, numerous similar looking species of *Pseudozaphrentis* or of the genera mentioned above may be compared with the Karakorum population.

The new species shows close resemblance to *Mictophyllum modicum* Smith, 1945 from the Frasnian of Canada. Specimens of its type-series (Smith 1945: pl. 5, fig. 1-2, 4-6; the specimen on his pl. 5, fig. 3 may be assigned to *Piceaphyllum* and the specimens figured as "near *modicum*" may belong to *Temnophyllum*) show slightly longer major septa that reach to the corallite axis and a stronger tendency to develop presepiments (compare McLean 1993, p. 114, figs 2.4-2.8). *Aulacophyllum ornatum* Soshkina, 1952 (Frasnian of the Russian Platform), is most probably conspecific with the Canadian species as it has comparably reduced minor septa and wedge-shaped septal bases. Some doubts concerning the synonymy of both taxa are indicated by a section of *A. orantum* in Soshkina (1954, pl. 2 fig. 4b), a weakly branching coral. In comparison to the Karakorum sample, both species differ in having longer septa and a tabularium that is predominantly composed of small tabellae.

Since its original description, *Mictophyllum modicum* has been recorded from many localities (Brice 1970; Soshkina 1951; Liao 1977; Tsyganko 1981), but definite assignment to the Canadian form is impossible or very unlikely for morphological reasons; the accuracy of those records has to be questioned. The Russian samples of Soshkina (1951, p. 58, figs 24-25, pl. 8, figs 6-7, pl. 9, figs 24-25) differ from the Karakorum species in having longer and strongly spindle-shaped septa. Another member of this group is *Mictophyllum guniae* Różkowska 1979, from the Upper Devonian of Mokrzeszów/Oberkunzendorf (Sudetes). It has a much smaller diameter than the Karakorum species. Without doubt, *Aristophyllum simakovi* Bul'vanker et al., 1975 is another closely related species, but differs by its higher septal number and larger corallites.

Pseudozaphrentis is widely distributed in the Devonian of China; numerous species are closely similar to the specimens from Siru Gol. *Temnophyllum wangyouense* Kong, 1978 (Givetian of Guizhou) is known from only a single section figured in Kong & Huang (1978, p. 97, pl. 33, fig. 1) and can not be sufficiently characterized. The figured section is very close to the material described herein and differs only slightly in its thicker septa, which may expand peripherally to form a narrow septal stereozone at the corallite wall, covering some parts of the dissepimentarium in longitudinal section. Its original classification as *Temnophyllum* seems to be reasonable. Characterization of *Sinodisphyllum yungxiense* Ouyang, 1983 in Cao et al. (1983, p. 80, pl. 24, fig. 3) is also problematic, but the species seems to differ in its higher number of septa. *Pseudozaphrentis wangchengpoensis* Yu & Liao, 1974, can be separated by its smaller diameter and a higher number of septa. (see Liao 1977, p. 45, pl. 2, figs 1-2; Liao & Birenheide 1989, pl. 2, figs 8-10).

Another group showing similarities includes *Pseudostringophyllum miniarense* Soshkina, 1939. Pedder (1972) has regarded this species as *Temnophyllum*, but numerous specimens which were placed in this genus have reduced minor septa, replaced by herring-bone dissepiments, as in *T. lenzi* Pedder, 1972 from the Ramparts

Formation, District of MacKenzie, close to the Middle/Upper Devonian boundary beds. An assignment of such forms to *Pseudozaphrentis* seems justified.

Family Columnariidae Nicholson, 1879

Subfamily Columnariinae Nicholson, 1879

Disphyllum deFromentel, 1861

Type species: *Cyathophyllum caespitosum* Goldfuss,1826.

Disphyllum cf. **caespitosum caespitosum** (Goldfuss, 1826)

Lectotype, locus typicus, stratum typicum and diagnosis. See Birenheide 1969, p. 38.

Material. MPUM 9125; CK 377, Yarkhun River Section, SW of Gharil.

Remarks. The fragment of a phaceloid corallum consists of only a few corallites with a rather large diameter of 10-12 mm and a constant number of 26 major septa. The major septa do not reach to the corallite axis, leaving a large axial space free, whereas minor septa reach about ½ of the radius. The specimen corresponds well to *D. caespitosum*, but has a slightly smaller tabularium diameter. As the available longitudinal sections are insufficient, a definite assignment to that species is questionable.

A similar species is "*Pseudostringophyllum*" *caespitosum* Soshkina, 1939 from the Frasnian of the Katav region, S Ural (compare discussion in Rohart 1999, p. 52), that differs only in its slightly shorter minor septa (Soshkina 1939, p. 36, 54, pl. 10, figs 81-82, pl. 12, figs 97-98).

Disphyllum caespitosum lazutkini (Ivaniya, 1953)

Pl. 1, figs 1-3

Holotype, locus typicus, stratum typicum and diagnosis. See Rohart 1988, p. 254.

Material. 11 corallites, MPUM 9144/1-11; CK 869: Siru Gol, SW of Lasht.

Description. Fragments most probably belonging to loosely phaceloid or dendroid colonies, consisting of slender cylindrical isolated corallites with a maximum observed length of up to 40 mm. In adult stage, corallite diameter ranges from 8-13 mm. Epitheca is well preserved and shows fine rugae or more rarely very faint longitudinal striae. In transverse section, septal bases may be slightly thickened and wedge-shaped near the corallite wall, but there is no development of a peripheral stereozone. Major septa range in number from 23-27 and are rather short, reaching to about 1/2 to 2/3 of the radius, so that a large space of 2.5-3.5 mm remains septal-free axially. Minor septa reach about 1/2 the length of the major ones and may rarely be replaced by a few herring bone dissepiments. All septa are generally thin or only weakly dilated and, especially within the tabularium, they are usually thread like. They are usually non-carinate although one corallite shows very irregular carinated septa. However, coarse carinae of the yardarm type are extremely rare. Dissepimentarium is narrow and consists of only 1-3 rows of small globose dissepiments, commonly traversed by the inward and upward oriented sections of coarse monacanths. They are usually globose but in some sections may become peneckielloid in shape. Tabularium is rather wide, with a diameter of 6-8 mm and consists of axially complete tabulae, flat at the centre but downturned at their margin. Periaxially they are supplemented with concave tabellae. There are about 10-15 tabulae/5 mm axially.

Remarks. The material here assigned to *D. caespitosum lazutkini* is typical in regard to its distinct tabularium structure consisting of convex ("trapezoidal") central tabellae and concave periaxial tabellae, described as "*lazutkini*-type" by Różkowska & Fedorowski (1972). Specimens are also closely comparable to the samples figured by Reed (1922, p. 14, pl. 2, fig. 12, pl. 3, figs 1-2) under the name *Cyathophyllum* (*Thamnophyllum* ?) sp. from Chitral. In longitudinal sections this species has also complete and convex central tabellae (pl. 3, fig. 1 is incorrectly oriented) concave periaxial tabellae and there is a narrow dissepimentarium. Soshkina (1939, p. 16) placed the Chitral specimens of Reed in her *D. caespitosum cylindricum* (Soshkina, 1939), although it differs in having much shorter septa of both orders and a "trapezoidal" tabularium structure. Most probably *Disphyllum lemaitreae* Brice, 1970 from the Givetian of the Helmand Block in Afghanistan belongs to the same group; it differs only slightly in having even more reduced minor septa (Brice 1970, p. 271, pl. 15, figs 9-13).

In the description of *Disphyllum caespitosum tricyclicum* Schouppé, 1965 from Chitral, separated from the nominotypical subspecies by development of third order septa, Schouppé (1965) refers among others to the abovementioned specimens of Reed. However, Reed´s specimens do not show any traces of a third-order septal cycle and the central tabulae of *D. caespitosum tricyclicum* are not strongly differentiated from the usually dissepiment-like periaxial tabellae. It is necessary to reconfirm the existence and constancy of such third-order septal traces, especially in regard to the small number of specimens (3) on which Schouppé based his studies. At this time it cannot be excluded that the structures figured by Schouppé (1965, fig. 2, pl. 1, figs 2-4) are diagenetically induced or were caused by a secondary thickening of the septa and coral wall.

Following the description of Schouppé, only Cheng (1969, p. 71) and Rohart (1999, p. 52) have recently applied the name *D. tricyclicum* to *Thamnophyllum*-species from Spain and Iran. Rohart's assignment to this species was based - apart from general morphological similarity - largely on recognition of third-order septa in his specimens, discussed and explained in connection with the term "hyposepta". Rohart explicitly stresses the irregularity and incompleteness of the third order-septa in his material, with and without such septa. As a matter of fact, there are indeed

insertions of wedge-shaped structures between the septa in some transverse sections figured by Rohart (1999, pl. 7, fig. 2c, 3b-c). Some seem to possess a dark median line and interrupt the neighbouring major or minor septa, so that the septal bases seem to be cut at a high angle towards the exterior and no longer reach the epitheca. Accepting such structures as true primary skeletal elements implies that neither major nor minor septa were directly inserted at the wall or that such an insertion was at least discontinuous. However, these "septa" are extremely irregularly developed; it cannot be completely excluded that they are caused by diagenetic effects. Not all septa are affected by these structures and a dark median line may also be the result of "Kristallisationsfronten" which may appear not only close to the wall, but at any place where septa are in lateral contact. Numerous examples of similar phenomena are known especially from species generally affected by strong skeletal thickenings, such as *Dendrostella trigemme* (Quenstedt, 1879), in which so called "Wandkeile" are common structures causing development of pseudoseptal structures (Oekentorp-Küster & Oekentorp 1992, pl. 7, fig. 4).

Coen-Aubert (1995, p. 42) places *D. c. tricyclicum* within the genus *Peneckiella* Soshkina, 1939 as its dissepiments are sometimes slightly inflated and upturned (Schouppé 1965, fig. 4), very similar to typical peneckielloid dissepiments. *Disphyllum* and *Peneckiella* are very similar and may be separated in some cases only because of their different trabecular structure. Unfortunately trabeculae are not recognizeable in the figures of Schouppé, but in his description he explains the structure within the longitudinal sections as "von außen-unten nach innen-oben gerichtete parallele Trabekelreihen" which in no way indicates the development of rhipidacanth trabeculae.

Occurrence. Widely distributed in the Frasnian of Europe (Spain, Poland, Belgium, France), Algeria, the Kuznets-Basin, the Elburz part of the Northwest Iranian Plate and the Karakorum Mtns.

Disphyllum sp.

Pl. 9, fig. 3

Material. MPUM 9126; Yarkhun River Section, SW of Gharil.

Description. The fragment of a phaceloid corallum consists of small corallites ranging in diameter from 8 to 10 mm. Corallites are characterized by an incomplete stereozone of wedge-shaped septa close to the outer wall, and especially of additional stereome developed near the tabularium boundary. Major septa number constantly 25 to 26 and extend to the corallite axis. In some corallites a small axial space of 1 mm may be left open. Minor septa are much shorter and only rarely enter the tabularium, which has a diameter of 4-6 mm and is clearly biseriate. Axially it is composed of horizontally arranged tabulae with downturned edges, periaxially supported by inclined or concave tabellae. The dissepimentarium is rather narrow and consists of 1-2 rows of globose to slightly peneckielloid dissepiments arranged in a flat or even upturned series, only rarely inclined toward the corallite axis.

Remarks. Even though *Disphyllum* is a widely distributed genus including numerous species, it is not possible to assign the single specimen to an already known taxon. However, within a species group characterized by long septa, *Disphyllum virgatum* (Hinde, 1890) described from the Frasnian of the Canning Basin in W Australia shows a close resemblance.

Whereas typical specimens of that species differ in some features of the longitudinal section, usually composed of a broad dissepimentarium of axially inclined dissepiments and of more incomplete tabulae, there are some specimens questionably assigned to that species, which are rather similar to the Karakorum specimen. Two examples with this type of morphology are a specimen of Hill & Jell (1971, pl. 9, fig. 6) asssigned to *D. virgatum* and also *Disphyllum virgatum* var. *densum* Hill, 1954; both have upturned series of dissepiments and rather complete tabulae. *Disphyllum hsianghsienense* Yoh, 1937 is also characterized by a distinct inner wall of thickened septa and dissepiments, but differs in having concave tabellae in the central part of the tabularium. Specimens of this group with development of a peripheral stereozone have been placed in *Solominella* Ivaniya, 1952.

Subfamily Hexagonariinae Bul'vanker, 1958

Hexagonaria Gürich, 1896

Type-species (subsequent designation by Lang, Smith & Thomas 1940): *Cyathophyllum hexagonum* Goldfuss, 1826.

Hexagonaria cf. **sanctacrucensis** Moenke, 1954

Pl. 8, fig. 1; Pl. 9, fig. 6

Material. One fragment of colony MPUM 9145; CK 869: Siru Gol, SW of Lasht.

Description. The fragment of a cerioid corallum is 10 x 10 cm and consists of medium sized, polygonal corallites with a diameter varying from 7-9 mm at the adult stage. Septa are generally inserted at the wall and are not interrupted by any lonsdaleoid dissepiments. They are typically slightly dilated in the inner dissepimentarium, but become very thin within the tabularium and especially when approaching the corallite axis. In contrast to the long major septa, which number 19-21, leaving open only a small axial space of 0.5-2 mm diameter, minor septa are much shorter with a length of about ½ of the radius. Within the dissepimentarium most septa are "carinate". The carinae are developed as small irregular carinae-like septal structures which may appear as zigzag-carinae in corallites with thin septa. In corallites with more strongly

dilated septa, trabeculae are more dilated and may resemble coarse yardarm-carinae. Carinae are rare or may be lacking almost completely in juvenile corallites.

In longitudinal section, tabularium is rather narrow ranging from 4-5 mm diameter. It is composed of slightly convex central tabulae flanked by periaxial rows of tabellae. The narrow dissepimentarium consists of a few rows of small bulbous dissepiments, inclined near the tabularium but rather flat near the wall. This arrangement is followed by sections of coarse monacanth trabeculae.

Remarks and occurrence. The specimen corresponds well to *Hexagonaria sanctacrucensis* Moenke, 1954, from the Devonian of the Holy Cross Mtns. However, there are only minor similarities with other European *Hexagonaria* species, except for *H. mae* Tsien, 1977, which has much longer minor septa reaching far into the tabularium.

Hexagonaria sp. **B**

Pl. 8, figs 3-4

Material. 2 fragments of colonies MPUM 9146/1-2; CK 869: Siru Gol, SW of Lasht.

Description. Material consists of two small fragments of cerioid colonies. Some of the polygonal corallites show calices with a flat calicinal platform. The diameter of adult corallites is relatively large and the centres of neighbouring corallites are 9-14 mm apart. Septa generally thin peripherally, without traces of wall-thickenings. In the inner dissepimentarium, septa are usually slightly to strongly dilated and may bear carinae, which may be replaced by heavily swollen trabeculae. Number of major septa varies from 19-23. They extend almost to the axis where there remains only a small axial space of 2-3 mm free of septa. Minor septa are short and reach only to the boundary of the tabularium. They may be incomplete and interrupted in the outer dissepimentarium; there are no lonsdaleoid dissepiments. In longitudinal section the broad dissepimentarium is composed of elongate and horizontally arranged dissepiments which follow the morphology of a slightly everted calice. The tabularium has a diameter of about 5 mm and is filled with flat complete tabulae axially, flanked by axial concave tabellae.

Remarks. *Hexagonaria mirabilis* Moenke, 1954 from the Frasnian (Wietrznia) of the Holy Cross Mtns., is morphologically closest to this species, but differs in its smaller dissepiments arranged according to a more evert calice, and its longer major septa reaching to the corallite axis. The holotype of this species has been refigured by Coen-Aubert (1994, pl. 1, fig. 1-2). She regards *Hexagonaria mireillae* Rohart, 1988 to be synonymous. *H. crassiseptata* (Ivaniya, 1965) from the Frasnian of the Kuzbass (Siberia) is a closely related species which can be distinguished by longer and more strongly dilated septa. *Hexagonaria beichuanensis* (He, 1978) differs in having a narrow dissepimentarium consisting of smaller dissepiments.

Hexagonaria sp. **C**

Pl. 8, fig. 2; Pl. 9, fig. 4

Material. Corallum MPUM 9102; CK657: Border Ridge Section, NE of Lashkargaz.

Description. The strongly eroded fragment of a single corallum has a size of about 7x7 cm. Growth form of colony and corallite morphology are unknown. Adult corallites range in diameter from 15-20 mm. Intercorallite walls are straight, thin, and only slightly thickened by weakly dilated septal bases. In the outer dissepimentarium, septa are very thin but show a strong tendency to become spindle-shaped with dilations in their middle part. Slightly thickened septa usually bear irregularly arranged carinae which may be obscured by septal dilation, whereas in undilated septa there are only rare crenulations and no true carinae. Major septa number 24-25 and reach the corallite axis where they are very thin. Minor septa do not extend into the tabularium and have a length of approximately 2/3 of the radius. The tabularium (diameter 5-6 mm) contains convex tabulae and additional periaxial tabellae which are difficult to separate from the innermost rows of dissepiments. The dissepimentarium consists of numerous rows of small globose dissepiments, steeply inclined close to the tabularium but slightly everted in its external part. Sections of monacanthine trabeculae are common (Pl. 9 fig. 4) and reflect the slight reflexing of calicinal platforms.

Remarks. This is a species of *Hexagonaria* with large corallite diameters and moderately dilated septa, showing a close relationship to the type-species *Hexagonaria hexagona*. It differs in having a considerably smaller number of less dilated weakly carinate septa. It is also close to the holotype of *H. bassleri magna* (Webster & Fenton, 1924), recently revised in a very well illustrated monograph on the Frasnian fauna from Iowa by Sorauf (1998, pl. 32, figs 2-5); it belongs to a morphotype of *H. bassleri magna* with dilated septa. "*Prismatophyllum* cf. *magnum*" described by Brice (1970, p. 283) from Afghanistan corresponds quite well to this type with long, dilated and weakly carinate septa, it is very close to the specimen described here. "*Phillipsastrea*" *lazutkini* Bul'vanker, 1953 has a similar septal morphology but differs in its smaller corallites (Bul'vanker 1958, pl. 62, fig. 3; pl. 63, figs 1-3).

Hexagonaria sp. **D**

Pl. 9, fig. 5

Material. Corallum MPUM 9131; CK 377: Yarkhun River Section, SW of Gharil.

Description. The single examined specimen is a complete colony with a diameter of 15 cm and a thickness of 8 cm. It consists of remarkable large cerioid corallites that range between 15 and 20 mm, rarely 25 mm in the adult stage. Calices have a deep tabularial pit and wide flat peripheral platforms, which are not everted. As there are no dilations by septal bases, and septa are very thin peripherally, straight intercorallite walls are generally very thin. Number of major septa ranges from 21 to 24, reaching to the corallite axis or leaving only a small open space free of septa. Usually septa are very thin, thread-like and without any dilation. However, a few septa may show some weak spindle-shaped dilation within the inner dissepimentarium. They are always smooth and there are no carinae or other crenulations but may be slightly wavy within the outer dissepimentarium. Minor septa reach a length of 1/2 to 2/3 of the radius and are sometimes incomplete in their outer part. In longitudinal section, the dissepimentarium consists of medium sized dissepiments which are arranged flat in the outer part, but become steeply inclined when reaching the tabularium, where they are sometimes elongate. Sections of trabeculae are rare, but show the coarse monacanth structure typical for disphyllid corals. The tabularium is about 7 mm wide and contains axially convex tabulae flanked by smaller accessory tabellae.

Remarks. There are only a few species with large corallite diameter and thin noncarinate septa. The species is especially close to *Hexagonaria* sp. C, described above, from which it differs only by the much thinner and noncarinate septa. It can not be excluded that it is only a phenotype of the same species, as all other characters are more or less identical; this would be similar to the situation observed in *H. magna* by Sorauf (1998, p. 64), where two different phenotypes can be separated. The phenotype of *H. bassleri magna*, characterized by thin, noncarinate septa (Sorauf 1998, pl. 33, fig. 1) and including the western Canadian specimens described as *Prismatophyllum* cf. *magnum* by Smith (1945, p. 47-48, pl. 15, fig. 2-3) are very closely related to the corallum described here. *Hexagonaria ngariensis* Liao, 1982 from the Frasnian of Rutong, NW Xizang (Tibet) has similar measurements and septal morphology. However, the structure in longitudinal section and development of carinae of this species are insufficiently illustrated to allow closer comparison.

Argutastrea Crickmay, 1960

Type-species: *Argutastrea arguta* Crickmay 1960.

Argutastrea sp.

Pl. 9, fig. 2

Material. One colony Nr. MPUM 9149; CK 377: Yarkhun River Section, SW of Gharil.

Description. The fragment of a cerioid colony consists of numerous polygonal corallites ranging from 7 to 9.5 mm in diameter. Increase is nonparricidal, most probably lateral. Corallite walls are straight and sometimes slightly thickened by wedge-shaped septal bases. All septa insert at the corallite wall and number 19 to 22 in each order. They are typically slightly to moderately dilated within the dissepimentarium and, especially in the inner dissepimentarium, some additional stereome coats septa and neighbouring sections of dissepiments, though not building an inner septal stereozone. Within the tabularium, septa are very thin and become thread-like. Major septa usually extend to or almost to the corallite axis, but length of minor septa varies greatly. Although they usually extend about 1/2 the radius, in some cases they may be strongly reduced in length but are never replaced by herring-bone dissepiments. Dissepimentarium is variably developed and consists of only a few rows of globose dissepiments, but in some corallites it includes as much as 6 rows of slightly adaxially inclined elongate dissepiments. Tabulae are axially convex, have a downturned margin, and are usually supplemented with small globose tabellae.

Remarks. The specimen bears some resemblance to the fully cerioid specimens of *Argutastrea hullensis* Hill, 1945, especially from the Pillara Limestone of the Canning Basin, but differs from typical specimens in the absence of the peripheral sterozone usually observed in that species.

Phillipsastreidae Roemer, 1883

Phacellophyllinae Wedekind, 1921

Macgeea Webster, 1889

Type-species: *Pachyphyllum solitarium* Hall & Whitfield, 1873

Macgeea ? sp.

Pl. 1, figs 5-7

Material. Ten corallites, MPUM 9142/1-10; CK 869: Siru Gol, SW of Lasht.

Description. Corallites are preserved as short, slender cylindrical fragments. Growth is straight or slightly curved with a diameter of 10-13 mm; a few corallites show traces of axial budding. Corallite walls are usually eroded so that the thin epitheca and peripheral part of septa are frequently lacking. Thus, septa seem to insert in a dilated zone close to the outer wall, where they are spindle-shaped. This corresponds to the zone of thickened horseshoe dissepiments which are developed as a compact double wall and are typically convex/concave in transverse sections. Within this zone lateral dissepiments are not rare. Major septa number 25 to 28 and are rather long, reaching almost to the corallite axis, where a small space of 2-4 mm diameter remains septa free. In two corallites major septa are more strongly reduced and almost

equal the length of minor septa, reaching only slightly into the tabularium. Cardinal septum may be shortened. As epitheca and the outer dissepimentarium, consisting of small horizontal dissepiments, is usually eroded, the thickened walls of the horseshoe dissepiments form the apparent outer wall of corallites. Rhipidacanth trabeculae are commonly centered above the horseshoe dissepiments, usually arranged as a single pipe, but may be supplemented by 1-3 rows of small normal dissepiments adjacent to the inner wall. Tabularium diameter ranges from 7-8 mm and includes almost complete horizontal to slightly convex tabulae and are associated with small globose tabellae close to the thickened walls of horseshoe dissepiments. Tabulae are closely spaced with about 10 per cm.

Remarks. The material consists of short fragments of cylindrical corallites of generally small diameter and they may have belonged to a colonial form. Discrimination of isolated corallites from corallites of the solitary genus *Macgeea* is difficult, although most *Macgeea* species show a consistently larger corallite diameter. However, *Macgeea* also includes several species with smaller diameter such as *Macgeea desioi* Schouppé 1965 from Chitral, the Eifelian *M. bathycalyx* Frech 1886 or *M. recta* Walther 1928 which are known to develop similar long, cylindrical corallites and may be confused with fragments of *Thamnophyllum*.

Compared with *Thamnophyllum*, the described specimens have a rather large diameter and comparable high number of septa. Exceptions include *Thamnophyllum sinense* Yu & Liao 1974, which has about 28 major septa at a diameter of 11 mm, and the Frasnian *T. kozlowskii* Różkowska 1953. But the vast majority of *Thamnophyllum* species are generally much smaller in their dimensions.

Macgeea desioi is generally thought to be a solitary species (Rohart 1999) which closely resembles the specimens described above concerning biometrical data, but differs in its shorter major septa. However, septal length is known to be an extremely variable feature within *Macgeea*; the Siru Gol material includes sections with short and also long septa (Pl. 1, fig. 7). A juvenile [?] section of the holotype figured by Schouppé (1965, pl. 1, fig. 9) has also rather long septa.

Because of problems concerning growth form as well as septal length, it is not possible to assign the specimens with certainty to *M. desioi* or to a *Thamnophyllum* species, and it is here tentatively assigned to *Macgeea*.

Macgeea cf. **multizonata** (Reed, 1922)

Pl. 1, figs 8-10

Material. 9 corallites, MPUM 9143/1-9; CK 869: Siru Gol, SW of Lasht.

Description. Fragments of cylindrical corallites with maximum length of 50 mm at a diameter of 14-18 mm. All specimens are strongly weathered so that the epitheca is completely eroded. Accordingly, on the surface of weathered corallites the thickened zone of horseshoe dissepiments becomes visible, which is rather resistant to erosion. Septa are weak to moderately dilated and coated with stereome within this area, but are typically very slender when entering the tabularium. In contrast to the minor septa, which barely extend into the tabularium, major septa are longer but do not reach to the axis, leaving a small open area with a diameter of 3-5 mm. Major septa number 26-30 and are irregularly twisted within the tabularium. The cardinal septum is shortened in most of the corallites. In cross section horseshoe dissepiments are arranged convex/concave and are strongly dilated, so that a ring-like zone is present in most of the corallites. At the inner margin of this zone some dissepiments may be arranged in a herring bone pattern, which indicates that the row of horseshoe dissepiments is supplemented by 1-2 additional rows of normal dissepiments on their inner wall. These dissepiments are merging into globose or weakly elongate tabellae; there is no distinct border between them. The central part of the tabularium consists of flat or slightly convex tabulae, closely spaced at 10-20 tabulae per cm vertically.

Tabularium diameter is 8-10 mm. The external dissepiments are almost completely eroded in most of the specimens and only rarely are there remaining dissepiments which are platy and slightly inclined or even globose.

Remarks. Specimens show no major differences from the descriptions of *M. multizonata* given by Reed (1922) and Schouppé (1965). Biometrical data as well as septal morphology - rather short, slightly dilated and wavy septal ends - are closely comparable. They are determined as *M.* cf. *multizonata* as they differ from the diagnosis given by Coen-Aubert (1982) in having a slightly smaller corallite diameter and because of their insufficiently preserved outer zone of dissepiments.

Development of the outer zone of dissepiments is regarded as of high taxonomical value by most authors and typically includes platy as well as normal, globose dissepiments in *M. multizonata*. Development of this distinctive morphology is known from the colonial *T. supradevonicum* Penecke, 1903 [type-species of *Pseudopexiphyllum* Hubmann, 1992] or even stronger in *Macgeea* sp. B from the Frasnian Redknife Formation of Western Canada (McLean & Klapper 1989, pl. 1, figs 5, 8).

However, in most descriptions of *M. multizonata* specimens are weathered and the peripheral parts of corallites are usually not preserved. Reed (1922, p. 12) described this zone as "composed of a single row of straight horizontal dissepiments". In those sections of the type series (Reed 1922, pl. 2, fig. 3) with a sufficiently preserved zone of dissepiments, platy but slightly inclined dissepiments predominate, always clearly separated from the thickened walls of horseshoe dissepiments. The topotype figured by Lang & Smith (1935, pl. 37, fig. 15) is

abraded, but shows a clear development of vesicles flanking both sides of the horseshoes - not visible in the figures given by Reed.

M. rozkowskae Coen-Aubert, 1982 is a similar species but has longer, strongly dilated septa, almost reaching to the corallite axis, and horseshoe dissepiments not associated with globose or elongated normal dissepiments on their external side.

Macgeea cf. **gallica gigantea** Brice & Rohart, 1974

Pl. 1, fig. 11; Pl. 2, fig. 1

Material. 2 corallites MPUM 9123/1-2; CK658: Border Ridge Section, NE of Lashkargaz.

Description. Two fragments of large solitary coralla with a maximum diameter of 36 mm and a length of 60 mm. In cross-section, major septa range from 46 to 48 and are withdrawn from the axis, where a septa-free space remains. Axial ends of septa are usually slightly undulating. Cardinal septum is reduced in length and lies in a well developed fossula. In one specimen, additional alar-fossulae are developed. Peripherally, septa are very thin, but are strongly dilated in the zone of horseshoe dissepiments and reach their maximum thickness within this area. Within the tabularium they are slender again. The zone of horseshoe dissepiments appears very wide and contains, in addition to sections of thickened horseshoes, common lateral dissepiments. With a length of about 1/2 to 2/3 of the radius minor septa barely extend into the tabularium where numerous sections of dissepiments flank the thickened inner wall of the horseshoe dissepiments. In juvenile stages, minor septa do not enter the tabularium. They are usually dilated and commonly their septal ends are thickened by additional stereome. Tabularium reaches a maximum diameter of 29 mm. It is composed of a central series of closely spaced tabulae, horizontally to slightly convex, with downturned edges and a zone of peripheral tabellae, merging with a narrow zone of elongate inner dissepiments. Vertically there are up to 24 tabulae per 10 mm.

Zone of horseshoe dissepiments consists of large and broad vesicles, usually slightly displaced from each other, so that different sized vesicles overlap. The outer wall of this zone is distinctively thickened. Adjacent to this wall there is a very narrow layer of outer, platy or slightly globose dissepiments.

Remarks. Only a few comparable large and septal rich species of *Macgeea* have been described of which *M. gallica gigantea* is the most similar one. The holotype (Brice & Rohart, 1974, pl. 8, fig. 1a) has slightly longer major septa reaching almost to the corallite axis and are moderately dilated throughout. One paratype specimen (Brice & Rohart, pl. 8, fig. 4a) is more closely comparable to our material in this respect, but specimens from the Shogrâm Formation typically have dilated septa in early ontogeny (not figured for *M. gallica gigantea*) and a wider tabularium. Wang (1994, p. 450, pl. 46, fig. 2) assigns a specimen from the Upper Givetian of W Yunnan with strongly dilated septa to *M. gigantea* and awards it full species rank. The holotype of *M. telopea* Crickmay, 1962 (pl. 2, figs 12-13) from the middle Frasnian Grumbler Formation of the Northwest Territories (Canada) differs only slightly in its peripherally thinner and shorter minor septa, replaced by common herring bone dissepiments. *M. araxis* Frech, 1900 *sensu* Soshkina 1952 (pl. 18, fig. 64) from the Givetian of Armenia is insufficiently described to allow closer comparison, but seems to differ in the strongly developed globose dissepiments in its outer dissepimentarium (Sytova & Ulitina 1974, p. 31, pl. 1, fig. 2).

Cyathophyllum birmanicum Reed, 1908 from Middle Devonian limestones of Padaukpin (Myanmar) is a similar large coral with numerous septa and a well developed fossula, which belongs most probably to *Macgeea* as Reed figures rhipidacanth trabeculae in one longitudinal section and describes the outer part of the dissepimentarium to consist of "fairly regular nearly vertical smaller and less convex vesicles" (Reed 1908, p. 6). Wright (1995) lists the species as a *Macgeea*. But the row of horseshoe dissepiments is not well developed in the figured longitudinal section, and the outer platy dissepiments are lacking. Jell & Hill (1969, p. 11) regard *C. birmanicum* as belonging to the predominantly Lower- to Middle Devonian *Gurievskiella* Zheltonogova, 1961. The genus was temporarily included in the Phillipsastreidae because of its conspicious "fan-like" trabecular structure (Jell 1969; Jell & Hill 1969), but has lately been assigned to the Paradisphyllidae Jell 1969. In addition to the missing series of outer platy dissepiments, the genus differs from *Macgeea* in having a highly arched dissepimentarium and a non-differentiated cardinal septum. However, the more or less constantly developed horseshoe dissepiments, usually arranged in a single pipe in small species, sometimes breaks down in larger species.

A group of species in which horseshoe dissepiments are completely absent in adults is included in *Macgeea* (*Rozkowskaella*) Wrzołek, 1987; it includes *Macgeea* (*Rozkowskaella*) *formosa* (Różkowska, 1979), the type-species of *Debnikiella* Różkowska, 1979. This Upper Frasnian species is still insufficiently known, but as far as interpretation of available figures allows (Różkowska 1979, p. 25, fig. 5), it shows close resemblance to the specimens described herein, but has a smaller diameter, a lower number of septa and a strongly everted calice.

Pseudopexiphyllum Hubmann, 1992

Type-species: *Thamnophyllum supradevonicum* Penecke, 1903

Remarks. *Pseudopexiphyllum* has been introduced to accomodate forms with an internal morphology similar to that of *Macgeea* or its synonym *Pexiphyllum* Walther,

1928, but different in having a phaceloid growth form. In particular, Hubmann (1992, p. 160) regards the development of several rows of additional dissepiments on both sides of the series of horseshoe dissepiments as a main diagnostic feature of *Pseudopexiphyllum*. In this regard it differs also from *Thamnophyllum* Penecke, 1894, which has an outer dissepimentarium composed of predominantly platy and flat dissepiments, sharply separated from a usually narrow row of horseshoe dissepiments. Generally, species of *Thamnophyllum* can be distinguished by their much smaller corallite diameter.

A generic classification of phillipsastreid corals, based on the presence or constancy of internal dissepiments, bordering the inner wall of the horseshoes, is difficult to establish because of the considerable variation observed in the development of such dissepiments. It has been repeatedly shown that the separation of *Macgeea* and *Pexiphyllum* is impossible on grounds of the presence of such dissepiments (Schouppé 1958, p. 223; McLean 1989, p. 245). A similar high variability is known to affect the development of the horseshoe dissepiments; a proposed generic separation of the closely related genera *Phillipsastrea* d'Orbigny, 1849 and *Medusaephyllum* Roemer, 1855 was rejected.

Since its erection, *Pseudopexiphyllum* has been known as a monospecific genus, containing only the enigmatic type species *Thamnophyllum supradevonicum* Penecke, 1903. Apart from the type specimens, some additional (probably topotypic) samples from the vicinity of Feke in the Turkish Antitaurus were subsequently included, but so far the species has not been recorded from anywhere other than Turkey. Other species are not known, and there are only a few examples of Devonian corals that show comparable morphology.

A Lower Devonian specimen of *Phacellophyllum furcosum* var. *maius* Pedder, 1970 illustrated by Jia (1977, pl. 51, fig. 3) from China appears to be morphologically close to *Pseudopexiphyllum* because of its arched series of small dissepiments. Jia assigned it to his genus *Parasulcorphyllum* Jia, 1977, although typical specimens from the Lower Devonian Teamas Limestone of New South Wales, Australia, differ in having a more consistently developed row of horseshoe and outer platy dissepiments (Pedder et al. 1970, p. 241, pl. 48, figs 6-8), developed as in *Thamnophyllum*.

Parasulcorphyllum has been distinguished from *Sulcorphyllum* primarily by its different mode of dissepimentarial development (Jia 1977, p. 149). In fact the dissepimentarium of *Sulcorphyllum* is composed of platy and normal shaped dissepiments, which are - as can be observed in line drawings of longitudinal sections of its type species *Sulcorphyllum brownae* (Hill, 1942) - steeply abaxially inclined, ascending to a sharply separated single row of horseshoe dissepiments (Pedder 1964, text-fig. 2a; Hill 1981, fig. 182, 3).

The type-species of *Parasulcorphyllum*, the cerioid *Sulcorphyllum pavimentum* Pedder, 1970 from the Emsian Taemas Limestone of New South Wales, differs from the *Sulcorphyllum* morphology by its wide, strongly arched dissepimentarium that includes only occasionally true horseshoe dissepiments (Pedder et al. 1970, p. 242, pl. 48, fig. 3; pl. 49, fig. 4). However, taxonomical justification of the phaceloid to cerioid *Parasulcorphyllum* was questioned by Hill (1981), synonymizing it with *Sulcorphyllum* Pedder, 1964 and consequently with *Trapezophyllum* Etheridge, 1899.

Horseshoe dissepiments are irregularly developed within the arched dissepimentarium of *Pseudopexiphyllum* and a complete pipe of horseshoes is only rarely found, although a more or less contiguous series of variable sized dissepiments may be observed (Hubmann 1992, fig. 8b), reminiscent of the morphology known from *Parasulcorphyllum*. This unusual morphology may be relevant for separation from taxa with a narrow zone of continuous horseshoe dissepiments, and is most probably of generic significance.

Pseudopexiphyllum occultum n. sp.

Pl. 6, figs 1-3; Pl. 9, fig. 7

Holotype. MPUM 9130

Paratypes. 2 fragments of coralla, MPUM 9128-9129.

Locus typicus. N Pakistan, Yarkhun River Section S of Gharil, locality CK377 (see Talent et al. 1999, fig. 3)

Stratum typicum. Upper Devonian?, probably Frasnian or Late Givetian?

Derivatio nominis. latin, *occultus* = hidden, covered. Because of the long time of 100 years that has elapsed to discover a second species of *Pseudopexiphyllum*.

Diagnosis. *Pseudopexiphyllum* with large corallite diameter of 20-25 mm in gerontic stage and 29-33 major septa. Wide tabularium of closely spaced horizontal or slightly convex tabulae.

Description. Fragments of coralla are loosely fasciculate and most probably belong to large colonies, as individual corallites are rather thick and strongly budding. Colonies are formed by parricidal increase where 3 to more commonly 4 offsets arise simultaneously in the axial region of the mother corallite. Calices are not preserved, but from the weathered surface of one fragment it can be assumed that calical rims were everted. Diameter of a few gerontic corallites is very large and ranges from 20 to 25 mm, but usually fragments are composed of juvenile offsets having a diameter of 10 to 15 mm. The largest corallites have a maximum number of 29 to 33 major septa; at a diameter between 10 and 15 mm they number 22 to 25. In adults, major septa reach to or almost to the corallite axis where a small axial space of 3-5 mm may be left open. Axial ends of septa are usually thin and irregularly twisted, and the cardinal septum is shortened in most corallites. Minor septa reach a length of about ½ of the radius and do not enter the tabularium. They are sometimes incomplete peripherally, not inserting at the typically thin epitheca, but on sections of dissepiments (Pl. 6, fig. 3). Although septa show typically a weak to