# Hamaraxonia, a new pseudocolumellate genus of Middle Devonian deep-water Rugosa (Anthozoa) from Morocco

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**ABSTRACT.** The monotypic genus *Hamaraxonia* gen. nov., with type species *Hamaraxonia africana* sp. nov., is described, based on only four specimens, from the middle Eifelian (top *Costapolygnathus costatus* Zone to basal *Tortodus australis* Zone) of the Hamar Laghdad, Anti-Atlas, SE-Morocco. In its prominent axial boss and dissepiments in maturity, the new genus is unique among pre-Carboniferous ahermatypic Rugosa. It is classified within the still polyphyletic subfamily Columnaxoninae Weyer, 1980 of the family Cyathaxoniidae Milne-Edwards & Haime, 1850 (suborder Cyathaxoniina Spasskiy, 1977). Possible ancestors will probably be found among the neighbouring subfamily Laccophyllinae Grabau, 1928. For the moment, a phylogenetic line: *Laccophyllum* Simpson, 1900  $\rightarrow$  *Hamarophyllum* Berkowski, 2004  $\rightarrow$  gen. nov. pro *Cyathaxonia hercynica* Roemer, 1855 (Weyer & Zagora, 1990)  $\rightarrow$  *Hamaraxonia* gen. nov. may be proposed, pending further records from other regions and additional intermediate taxa. The commonly used term columella (aseptal origin) and the nearly forgotten term pseudocolumella (septal origin) are redefined in the already morphogenetic sense of their authors (Milne-Edwards & Haime 1848) by selecting morpho-terminological types: *Cyathaxonia cornu* Michelin, 1847 (late Tournaisian), and *Clisiophyllum keyserlingi* M'Coy, 1849 (middle/late Viséan).

KEYWORDS: Rugose corals, taxonomy, Cyathaxonia fauna, axial structure, Devonian.

# 1. Introduction

Long ago, small solitary Rugosa of the Cyathaxonia facies (sensu Hill, 1938) provided with an axial structure ("columella") were regarded as typical of Carboniferous and Permian coral communities. Hill (1956) classified them as three families of Cyathaxoniicae (suborder Streptelasmatina): Cyathaxoniidae, Lophophyllidiidae, Timorphyllidae. Hill (1981) accepted five families in two suborders for such taxa: Metriophyllina (Cyathaxoniidae, Metriophyllidae) and Plerophyllina (Lophophyllidae, Timorphyllidae, Verbeekiellidae). At present, further approaches towards a more natural phylogenetical taxonomy support the independent development of these "columellate" structures in ten Carboniferous-Permian familylevel units:

suborder Cyathaxoniina Spasskiy, 1977

Cyathaxoniinae Milne-Edwards & Haime, 1850 suborder Zaphrentoidina Schouppé & Stacul, 1959 (synonyms Metriophyllina Spasskiy, 1965; Stereolasmatina Hill, 1981; Hapsiphyllina Nudds in Nudds & Löser, 2001):

> Rylstoniinae Yü, Lin, Shi, Huang & Yu, 1983 Lophophyllidae Grabau, 1928 Variaxoninae Fedorowski, 2010 Lophophyllididae Moore & Jeffords, 1945 Timorphyllidae Soshkina in Soshkina, Dobrolyubova & Porfiriev, 1941 Verbeekiellidae Schouppé & Stacul, 1955 Wannerophyllidae Fedorowski, 1986 Lophotichiidae Weyer, 1972 Asserculiniinae Fedorowski, 1986

Radical changes in the stratigraphic aspect started with Różkowska (1969), who recorded *Cyathaxonia* Michelin, 1847 already in the Early and Late Famennian and its subgenus *Cyathocarinia* Soshkina, 1928 in the Late Famennian of Poland. Her species are now renamed *Cyathaxonia* (*Cyathaxonia*) *rozkowskae* Fedorowski, 2003 and *Cyathaxonia* (*Cyathocarinia*) *famenniana* Fedorowski, 2003. Similar collections occur in Germany (Weyer, 1984, 21, fig. 4/4-5) and in Morocco.

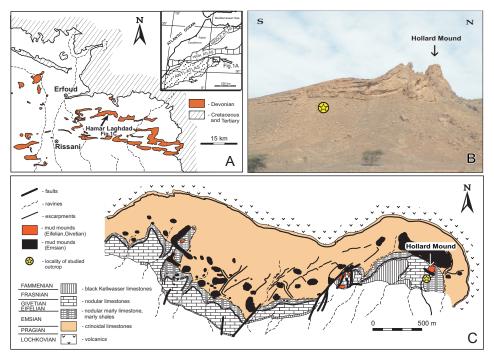
The next surprising discovery was *Columnaxon* Scrutton, 1971 from the Ludlowian of Venezuela. Then several Devonian "columellate" taxa were erected: *Famaxonia* Weyer, 1971 (Late Famennian, Germany), *Yishanophyllum* Wu & Liao, 1988 (Late Famennian, Guangxi province of China), *Cyathaxonia*? *hercynica* Roemer, 1855 = new genus (Weyer & Zagora, 1990, 27, fig. 3, Middle Givetian, Germany, meanwhile also found in France and Morocco), nov. gen. nov. sp. I (Weyer et al. 2003, 76, fig. 2D, Late Frasnian, Germany), *Cheilaxonia* Weyer 2004 (Early Famennian, Germany). In addition, there are further Devonian, unrevised species bearing an axial boss, as *Lophophyllum constrictum* Maurer, 1885 (Weyer 2005, 6, Middle Givetian, Germany) and *Lindstroemia stellata* Goryanov, 1967 (nomen nudum, mentioned in a faunal list of Goryanov & Klishevich (1968, 908), Pragian or Early Emsian, Kirgistan).

Actual systematics classified such pre-Carboniferous "columellate" genera into two subfamilies (Protozaphrentinae Ivanovskiy, 1959; Columnaxoninae Weyer, 1980) and as *incertae sedis*, probably all within the relatively deep-water representatives of the suborder Cyathaxoniina Spasskiy, 1977. Surely, this procedure is not reflecting real phylogenetic relationships and will be continuously emended according to urgently needed worldwide future studies of these "forgotten" rare corals in Silurian and Devonian times, and at the moment still completely unknown in the Ordovician (except for the stratigraphically curious genus *Protozaphrentis* Yü, 1957 from China).

Devonian Rugosa of the Cyathaxonia facies (ahermatypic, of dysphotic/aphotic and psychrospheric environments) are extremely poorly known in the Givetian (especially in its upper part after the Taghanic Event), in the complete Frasnian, and in the basal Famennian (time span of seven conodont zones, from Lower Palmatolepis triangularis to Uppermost Palmatolepis crepida). Perhaps, they are sometimes really rare (e.g. immediately after the Upper Kellwasser Event), but mainly they remained uncollected and unstudied. This explains the high number of Frasnian "silent taxa" (Wrzołek, 2002, including many "Lazarus taxa" and isolated "Elvis taxa"). Some of the few existing, mostly rather ancient literature data can be interpreted in the terms of actual biozonations only by stratigraphic insiders, and according to modern taxonomy only after intensive morphological revisions (e.g. Ludwig, 1865-1866; Weissermel, 1939).

Eight new Rugosa species of Ludwig (1865-1866) had been found in an iron ore horizon of the Mountains (Amplexus umbilicatus, Rhenish Amplexus breviradiatus, Anorygmaphyllum obtusum, Zaphrentis ampla, Hexorygmaphyllum radiatum, Liocyathus loculatus, Ptychocyathus excelsus, Taeniocyathus trochiformis). Their age is either Middle Givetian (Maenioceras terebratum Zone). Late Givetian (Pharciceras Genozone), or lower Frasnian. All these taxa are now invalidated (Opinion ICZN, 1971); none had ever been redescribed or could be identified using only the original illustrations, prepared before the introduction of thin sectioning techniques.

The six new taxa proposed in Weissermel (1939, based on badly preserved mould materials) are partly Late Frasnian (Hirtenrangen Formation – Zaphrentis curvatissima, Metriophyllum volki, Amplexus liliiformis), and partly Early Famennian (Plattenbruch Member of Bohlen Formation, Cheiloceras Genozone – Syringaxon thuringiacum,



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Figure 1. A: Simplified geologic map of northeastern Anti-Atlas, Devonian rocks and Hamar Laghdad are indicated; B: Outcrop marked by star in circle on southeastern slope of the "Hollard Mound" (view from the east). C: Detailed geological map of Hamar Laghdad with distribution of particular types of Devonian rocks. Star in circle indicates outcrop, where studied specimens were collected. Drawings A and C courtesy of Belka (1998 and unpublished) - updated.

*Combophyllum asteriscus, Lindstroemia? cornuhirci).* The author had noted the lithostratigraphical symbols (tob, toc) and bed numbers (in his plate explanations), indicated on the original labels of the collector Max Volk (1900-1969) and well explained in Volk (1939, with pelagic ostracod zonation). At present, most of these taxa seem to be undeterminable (especially in view of the probably lost type collection), excepting *Neaxon thuringiacus* (Weissermel, 1939) which is identical with *Amplexus pauciradiatus* Ludwig, 1865.

Here we describe the unexpected new pleonophorous genus *Hamaraxonia* from the Middle Eifelian of the famous mud mound area at the Hamar Laghdad, in continuation of the first monograph of Emsian deep water Rugosa in that region (Berkowski, 2008). This will be followed by the proposal of another "columellate" new genus, collected from Germany, France, and Morocco (Weyer & Berkowski, in preparation), rather strange in its mid-Eifelian to mid-Givetian occurrences and somewhat more reminiscent of the Permo-Carboniferous *Lophophyllidium* Grabau, 1928 (or its subgenus *Lophbillidium* Fedorowski, 1986).

# 2. Locality and Stratigraphy

The studied specimens were collected at the famous Moroccan locality Hamar Laghdad, in its eastern part called "Hollard Mound" (Fig. 1B). The Hamar Laghdad area is located approximately 18 km southeast from Erfoud city (Fig. 1A) in the easternmost part of the Anti-Atlas in southeastern Morocco. In this area, Devonian rocks dip gently southward and form an elongated W-E ramp where more than 50 conical buildups are perfectly exposed. The majority of the mounds are Emsian, but several of them cropping out in the most eastern side of Hamar Laghdad are either Eifelian or Givetian (Fig. 1C). Emsian mud mounds became the subject of extensive geological and palaeontological studies (e.g.: Roch, 1934; Massa et al., 1965; Hollard, 1974; Alberti, 1982; Brachert, et al., 1992; Wendt, 1993; Belka, 1998; Aitken et al., 2002; Berkowski, 2004, 2006, 2008, 2012; Belka & Berkowski, 2005; Cavalazzi et al., 2007; Berkowski & Klug, 2012). Belka (1998) and Mounji et al. (1998) related the formation of Hamar Laghdad mounds to hydrothermal venting activity. During the Early Devonian, submarine eruption formed an elevation on the sea floor, which subsequently became a site of extensive carbonate production. Conical mud mounds formed along synsedimentary faults that served as conduits for migration of hydrothermal fluids to the sea floor (Belka, 1998). Vents were episodically active during a time of approximately 30 Ma (from the Pragian until the early Frasnian). During the Eifelian and early Givetian, the subvolcanic activity persisted in the most eastern part of

Hamar Laghdad ("Hollard Mound") where hydrothermal fluids contained thermogenic methane derived presumably from the underlying volcanic intrusion (Peckmann et al., 1999).

"Hollard Mound" is located in the easternmost part of Hamar Laghdad (Fig. 1B) close to the complex of the easternmost Emsian mounds. On the eastern side it is cut by a fault, so its internal structure is well exposed. According to Peckmann et al. (1999, 2005) the deposition of the "Hollard Mound" carbonates started at the beginning of the Eifelian and ended by the end of the Givetian. These data are partly confirmed by detailed conodont stratigraphy of Hamar Laghdad, in preparation by Belka (personal comm.). The so-called "core of Hollard Mound" (sensu Peckmann et al., 1999) forms a large zone of sediments that exhibit isotopic signatures of hydrocarbon venting. They are composed of dyke fillings, vent deposits and carbonates related to venting activity. Fauna in the "core facies" is very diversified. The most conspicuous are clusters of large chemosynthetic bivalves and vestimentiferan tubes, which are located on the northeastern slope of the "Hollard Mound" (Peckmann et al., 1999, 2005), and monospecific Rugosa assemblages of Amplexus florescens (see Berkowski, 2006). The well-bedded sediments surrounding "the core" from the south (Fig 1B) include other numerous invertebrate taxa: i.e. cephalopods, gastropods, crinoids, trilobites, brachiopods, tabulate and solitary rugose corals.

Rugose corals described in the present paper were found within the well bedded nodular limestone covering "Hollard Mound" on its southern side (Fig. 1B). The beds are middle Eifelian in age and represent boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones (detailed stratigraphic investigation is now under preparation by Z. Belka).

## 3. Note on columella and pseudocolumella

In principal, the morphological glossary follows Hill (1981), though there a clear distinction between morphographic and morphogenetic terms is sometimes missing. Several emendations are already proposed (aulos: Fedorowski, 2009; septa: Weyer, 2008), and here - in view of the "columellate" new genus *Hamaraxonia*, unexpected in the Devonian - it seems necessary to start a similar procedure for the "columella" type of axial structures or axial bosses.

Milne-Edwards & Haime (1848a, 78) introduced the term **columella** for all skeleton-bearing corals (Scleractinia, Rugosa, Tabulata), but not alone: it was paralleled by another new term **pseudocolumella**, which nearly had been forgotten (even in the glossary of Hill, 1981). The main difference was seen in the genesis – septal origin in a pseudocolumella, non-septal origin in

a columella ("columella propria"). At present, it is appropriate to define such terms separately for Scleractinia and Rugosa, also using a "morpho-terminological type" genus/species (if possible, more or less in the sense of the original authors).

This is easy for "pseudocolumella", as Milne-Edwards & Haime (1848a) had already named the genus Clisiophyllum Dana, 1846 as an example. Thus we propose its genotype, the Early Carboniferous (late Viséan) Clisiophyllum keyserlingi M'Coy, 1849 as the definitive morpho-terminological type of the term pseudocolumella, which was already used in the description of that species (Milne-Edwards & Haime, 1851, 412). Future studies should subdivide this term for septal axial bosses using attributes other than the special structure of its type, characterizing many Ordovician to Permian taxa: e.g. Grewingkia Dybowski, 1873, Dinophyllum Lindström, 1882, Scenophyllum Simpson, 1900, Dibunophyllum Thomson & Nicholson, 1876, Ipciphyllum Hudson, 1958). Special sub-terms (comparable to those of Milne-Edwards & Haime, 1848a: columella septalis, parietalis, styliformis, fascicularis) are indispensable for other septal axial structures (pseudocolumella in wider sense), e.g. the mainly/exclusively antiseptal everted prolongation (with or without additional septal lamellae and tabulae) as in the genera Lophophyllidium Grabau, 1928, Rylstonia Hudson & Platt, 1927, Dorlodotia Salée, 1920, or Lithostrotion Fleming, 1828.

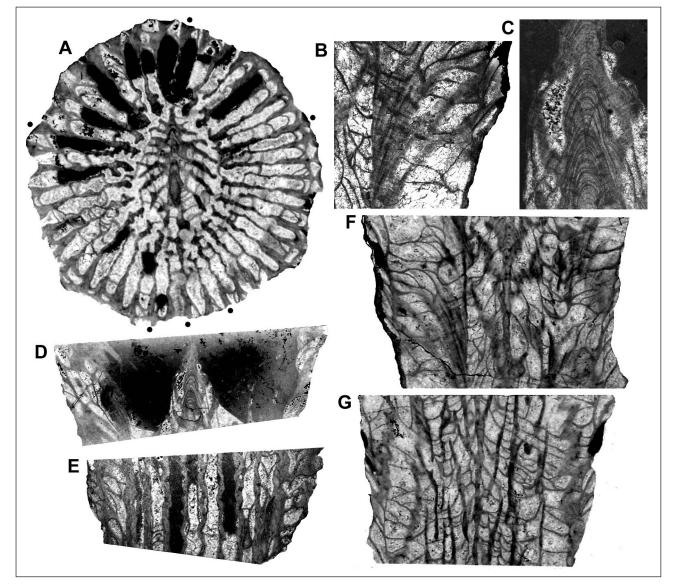
The term **columella** is defined within the superorder Rugosa by its here proposed morpho-terminological type

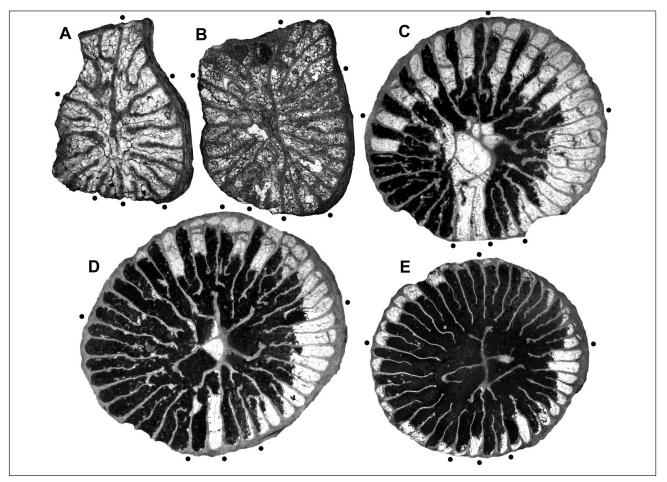
Cvathaxonia cornu Michelin, 1847 (Early Carboniferous, Late Tournaisian). Milne-Edwards & Haime (1848a, 79, pl.4/2a,1a) had mentioned only Scleractinian examples for their "columella propria" growing independently from septa, directly from the base of the skeleton: Turbinolia sulcata Lamarck, 1816 and Turbinolia dixonii Milne-Edwards & Haime, 1848 for a "columella propria styliformis", Turbinolia obesa Michelotti, 1838 (transferred by Milne-Edwards & Haime, 1848b to their new genus Trochocyathus) and Cyathina Ehrenberg, 1834 = Caryophyllia Lamarck, 1801, namely Caryophyllia cyathus (Ellis & Solander, 1786) for a "columella propria fascicularis". Later (Milne-Edwards & Haime, 1850, LXV, 1851, 163) ascribed "columella styliformis" to Cyathaxonia Michelin, 1847; а this justifies our morphological type choice. The columella of Cyathaxonia is a completely aseptal structure. Fedorowski & Vasilyuk (2011) described it as structure without any septal lamellae and developed tabulae-like sclerenchyme. Weyer (2001) simply interpreted this structure as an everted aulos, which shows only regular concentric growth lines in cross sections. By this redefinition, the axial boss of Hamaraxonia gen. nov. proposed here is a typical **pseudocolumella**.

## 4. Systematic Palaeontology

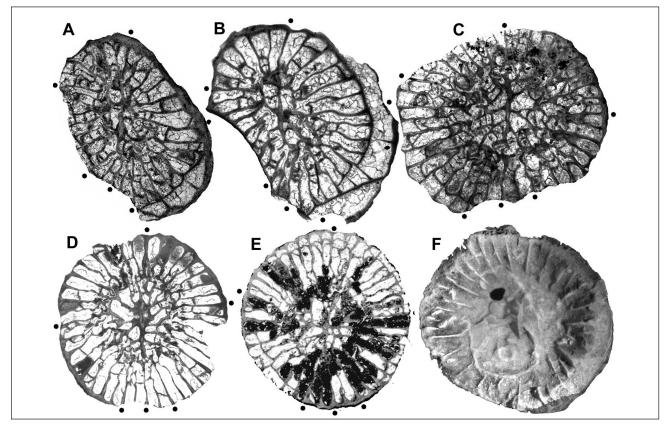
Abbreviations used: N = number of all septa, n = number of major septa (protosepta, metasepta), D = diameter, CS = cross/

**Figure 2.** *Hamaraxonia africana* sp. nov., holotype no. HD/0/A/2-6, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. A: CS13 at base of calice, x8, B: subtabular LS17, x12, with growth lines in a medially cut metaseptum, C: pseudocolumella of LS8, x18, D: calicular median LS4, x6, E: calicular tangential LS11, x8, F, G: subtabular median LS17, 20, x8, normal to cardinal-counter septal plane, with biform tabularium (inclination of tabulae adaxial in position I and abaxial in position II).



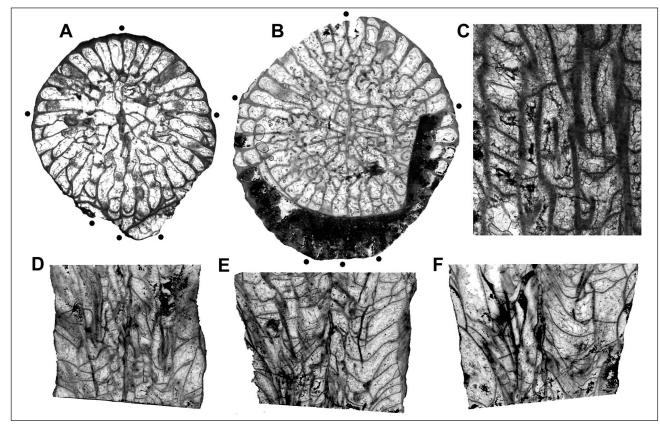


**Figure 3**. *Hamaraxonia africana* sp. nov., paratype no. HD/0/A/0-19, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. Ontogenetic series of 2 subtabular and 3 calicular CS, with well developed biform tabularium and first isolated mature dissepiments; A: CS12, x20, B: CS9, x18, C: CS 5, x10, D: CS4, x10, E: CS3, x8.



**Figure 4**. *Hamaraxonia africana* sp. nov., paratype no. HD/0/A/2-8, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. Ontogenetic series of 5 subtabular CS and free-weathered basal calice; A: CS8, x12, B: CS6, x12, C: CS4, x9, D: CS3, x7, E: CS1, x5, F: x6.





**Figure 5**. *Hamaraxonia africana* sp. nov., paratype no. HD/0/A/0-25, middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones, Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas), collection B. Berkowski 2001-2002 and 2010. A: subtabular CS26, x7, B: CS5, x6, older upper calice with again subtabular stage after rejuvenescense, C: slightly tangential LS9, x15, normal to cardinal-counter septal plane, with *Metriophyllum*-like carinae, D, E, F: median LS18, 11, 8, x5, oblique (D) and normal (E, F) to cardinal-counter septal plane, with opposite inclined tabulae of a strongly biform tabularium.

transverse section, LS = longitudinal section, TH = thin section, P = Peel, R = remaining part of corallum. Traditionally, six septa were marked; the cardinal septum is situated upside. All cross sections are presented in calicular view (from above); their orientation in an ontogenetic series is always equilateral (never reversed).

The studied corals are deposed in the collections of the Institute of Geology, Adam Mickiewicz University, Poznań (Poland), abbreviated UAM Tc/B HD/0/A/xx.

## Suborder Cyathaxoniina Spasskiy, 1977

Superfamily Cyathaxonioidea Milne-Edwards & Haime, 1850 Family Cyathaxoniidae Milne-Edwards & Haime, 1850 Subfamily Columnaxoninae Weyer, 1980

1980 Columnaxoninae nov. subfam.; Weyer, p. 1214. 2005 Columnaxoninae; Weyer, p. 7.

Genera included. Columnaxon Scrutton, 1971 (Ludlowian), Antilacca Weyer, 2005 (Late Emsian), nov. gen. nov. sp. I, Weyer et al., 2003 (Late Frasnian), nov. gen. pro Cyathaxonia? hercynica Roemer, 1855, Weyer & Zagora, 1990 (Middle Eifelian— Middle Givetian). Surely, these taxa constitute an at least partly polyphyletic assemblage to be reclassified (at subfamily level) after better understanding their true relationships. The source is mainly among the ancient family members, the Laccophyllinae Grabau, 1928.

#### Genus Hamaraxonia gen. nov.

*Derivation of name*. From the name of the North African locality Hamar Laghdad (Morocco) and presence of an axial structure.

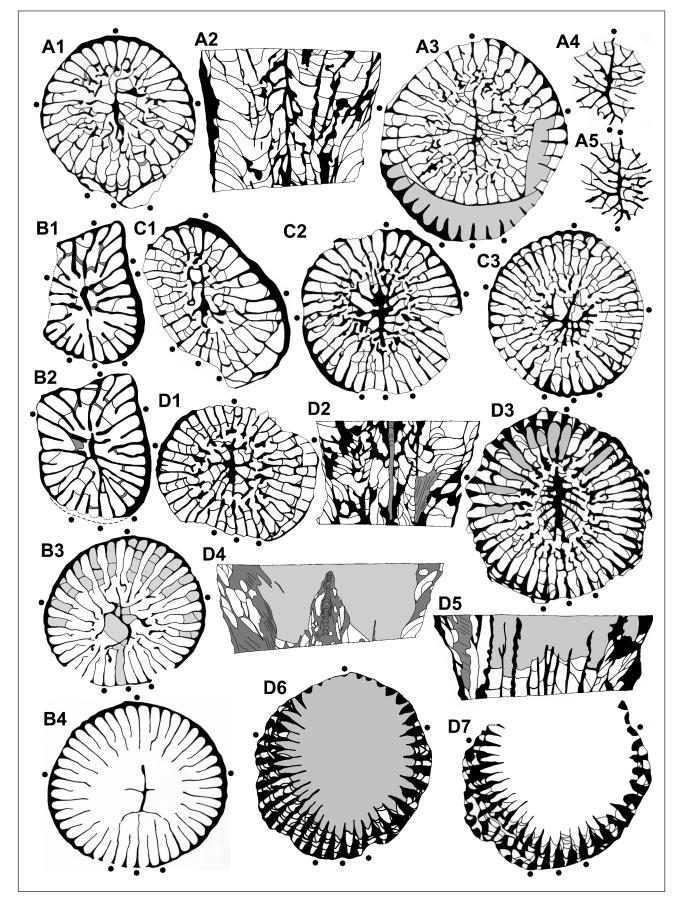
#### Type species. Hamaraxonia africana sp. nov.

*Diagnosis*. Small long-conical pleonophorous corallum with a deep calice bearing a high pseudocolumella, which starts with a primary cardinal-counter lamella and finally has many additional septal lamellae (only a little less than the number of long major

septa) with many steep tabulae. The long, radially arranged major septa, all (including the cardinal septum) of equal length, join the pseudocolumella a few times in juvenile phases; during middle growth stages their axial ends become free and slightly thickened, later at maturity often with irregular bifurcations or even trifurcations. The rather long minor septa are contraclined, never contratingent. Septal flanks with flanges parallel to the distal margin of septa, sometimes with few metriophylloid carinae. There is only an extremely weak stereoplasmatic thickening of the complete septal apparatus; interseptal spaces are always much wider than the thin septa. Tabularium strongly biform, with contrary inclined tabulae in position I (centripetally) and position II (steeply centrifugally). A normal concentric dissepimentarium (1-3, maximally 5 rows) arises in adult stages; very rare lonsdaleioid dissepiments are perhaps related to rejuvenescence.

Relationships. The peculiar combination of diagnostic features is unique among Rugosa. At present, the only probable ancestor will be a still not described other new genus, already mentioned by Weyer & Zagora (1990), based on a hitherto unrevised Middle Givetian ancient species from the German Harz Mountains, Cyathaxonia hercynica Roemer, 1855. We are now preparing the revision (based on a rich topotype collection) of this taxon (with a massive pseudocolumella, without dissepiments), which also occurs at the same level of the German Rhenish Mountains, in the Lower Givetian of the Montagne Noire (France), and in the Middle Eifelian-Middle Givetian of the Hamar Laghdad (Anti-Atlas, Morocco). A possible phylogenetic line Laccophyllum Simpson, 1900 → Hamarophyllum Berkowski, 2004 → gen. nov. (pro Cyathaxonia hercynica Roemer, 1855) → Hamaraxonia gen. nov. is proposed, indicating a doubtless origin from the subfamily Laccophyllinae Grabau, 1928, and waiting for future emendations after the discovery of additional, still unknown intermediate generic taxa.

*Occurrence*. At present, monotypic in the Middle Eifelian of Morocco.



**Figure 6**. *Hamaraxonia africana* sp. nov., middle Eifelian, boundary beds of upper *Costapolygnathus costatus* and lower *Tortodus australis* zones; Hamar Laghdad Ridge (eastern slope of Hollard Mound) ESE of Erfoud (Tafilalt, Anti-Atlas); collection B. Berkowski 2001-2002 and 2010. A: paratype no. HD/0/A/0-25; A: subtabular LS26, x6, with an early rejuvenescense near counter septum, A2: subtabular median LS 11, x5, normal to cardinal-counter septal plane, A3: mature CS5, x5 (supratabular areas light grey), A4, A5: septal lamellae and tabulae of the pseudocolumella in CS2, CS1, x5. Photos see Fig. 5A-F. B: paratype no. HD/0/A/0-19; juvenile subtabular (B1, B2, x12) and adult calicular (B3, B4, x6) ontogenetic series of CS (no. 10, 9, 5, 1); light grey regions in B3 are subtabular. Photos see Fig. 3A-E. C: paratype no. HD/0/8/2-8; successive subtabular LS17, x5, normal to cardinal-counter septal plane, D3: CS13 at base of calice, x5 (light grey areas are calicular), D4, D5: lower calicular median and tangential LS (no. 8, 7), x5, normal to cardinal-counter septal plane, D6, D7: upper calicular CS (no. 2, 1), x4. Photos see Fig. 2.

New Middle Devonian pseudocolumellate coral genus from Morocco

*Hamaraxonia africana* sp. nov. (Figs 2-6)

*Derivation of name.* After the African locality where the type species was found.

*Holotype*. Specimen no. HD/0/A/2-6. =10CS(4TS,6P),16LS(9TS,7P),1R. (1 duplicate peel (cross section no.12) in Berlin (Museum of Natural History, no. MB.K.7939.)) - Figs 2A-G, 6D1-7.

*Type locality*. Hamar Laghdad Ridge ESE of Erfoud, eastern slope of Hollard Mound (Tafilalt, Anti-Atlas, Morocco).

*Type horizon*. Middle Eifelian, boundary beds of upper part of *Costapolygnathus costatus* Zone, and lower *Tortodus australis* Zone.

Paratypes. 3 specimens, all – as the holotype – collection B. Berkowski 2001-2002 and 2010. 1. no. HD/0/A/0-19.=12CS(6TS,6P),2R. Figs 3A-E, 6B1-4. 2. no. HD/0/A/0-25.=14CS(6TS,8P),12LS(7TS,5P),1R. Figs 5A-F, 6A1-5. 3. no. HD/0/A/2-8. =8CS(5TS,3P),3R. Figs 4A-F, 6C1-3.

*Diagnosis*. For the moment, identical with that of the still monotypic genus.

*Description*. The small long-conical corallum is straight and/ or irregularly cornute (length 20-25 mm, calicular D 9-14 mm). The normally damaged proximal tip (minimal observed D 2.5 mm) was fixed by a tiny talon (Fig. 6B1); in addition, once a root-like outgrowth was present just above the talon. In the case of curvature (Fig. 3), the cardinal septum is situated on the convex side. Weak rejuvenescense may occur sometimes (Figs 4, 5). The archaeotheca bears fine growth rugae and distinct weak longitudinal septal furrows (Fig. 6C3) of protosepta, metasepta, and catasepta, but not of hyposepta; interseptal ribs are narrow and rounded to nearly sharp.

Mature calices with a slightly thickened wall have a prominent pseudocolumella occupying about one third of D. A primary, hardly ever thicker cardinal-counter septal lamella (Figs 2C, D, F) is connected with thin, occasionally bifurcating septal lamellae, more or less corresponding to the number of major septa (Fig. 6A3-5), but sometimes excepting the last one in a quadrant, which usually appears like a minor septum (Figs 6C2, 6D3). A section near the top of the pseudocolumella (Fig. 6B4) shows only 6 septal lamellae of the protosepta. The structure becomes delimited by steeply (up to vertical) inclined tabellae (Fig. 6D4), passing over to the normal tabularium. During juvenile stages (Fig. 6B1-2), only the cardinal-counter septal lamella is present; then in middle growth phases those of further major septa appear slowly.

The adult septal apparatus consists of 40-44 thin, radial arranged septa:

<u>4 4</u> n 24, N 40	<u>5 5</u> n 26, N 44	<u>4 4</u> n 26, N 44
6 6 D 11 mm	6 6 D 8-8.8 mm	7 7 D 10.4 mm
Fig. 6A3	Figs 6B4, 6C3	Fig. 6D3

They start at the calicular rim with a broadly rounded base (Fig. 6D6) that later becomes (for the greater part) incorporated into the somewhat thickened wall. After growth in the calice (growth lines visible in Figs 2B, 6D4), the major septa nearly reach the pseudocolumella, but retain their free axial ends – some few connections are visible only in the extreme youth (Fig, 6B2). All major septa (except the last one of every quadrant) have the same length; also the cardinal septum is never shortened. The slightly thinner, rather long minor septa reach about 75 % of the major septal length; they are never contratingent, but always contraclined (seen by the biform tabularium, not in any inclination towards the antiseptal/counter side). Stereoplasmatic thickening of all septa is always minimal; interseptal lumina are much wider (except the broad dissepiment zone in Fig. 6D6-7 after a rejuvenescense). Septal flanks bear a weak "ornament" of flanges (parallel to the distal margin) and rare metriophylloid carinae (Figs 5C, 6A3, 6D5). A strange mature specialisation occurs in most major septa: their thickened, sometimes nearly rhopaloid axial ends show irregular bifurcations or even trifurcations in cross sections; a conceivable explanation as palilike structures, initially suggested by locally everted tabellae in Fig. 6D2 (upper right tabularium), could not be verified. The septal microstructure is lamellar (term of Schindewolf, 1942; a synonym is "fibronormal" of Kato, 1963); the distal septal margins are smooth (Figs 2B, 6D6) and do not bear trabecular spines.

The tabularium is strongly biform, with different inclination and type, in position I (*sensu* Sutherland 1965) centripetally, dominant tabellae; in position II centrifugally, dominant simple tabulae). This is well seen in subtabular sections, both LS (Figs 5E, 6A2) and CS (curvature of tabular intersections convex towards the wall in position I, concave in position II). The calicular base (Figs 3C, 6D3) demonstrates this by the regular different filling of the interseptal spaces, alternately either with sparite or with detritus. The height difference between the uppermost tabulae in position I and II can be estimated in Fig. 6D4.

A narrow dissepimentarium of normally 1 to 2, rarely 3 rows of vesicles arises at maturity. The first appearance in Fig. 6C2 (D 7 mm, left antiquadrant/counterquadrant) is recognizable by the curvature of the intersection in position II (convex towards the wall); later (Fig. 6C3) there exists one regular row of concentric vesicles between most major and minor septa. The broader dissepimental zone in Figs 6D6-7 (up to 5 rows) is an exception restricted to a rejuvenescence zone, which also caused some few lonsdaleioid vesicles (Figs 4B, 6A1, 6D7).

*Discussion.* The smallest paratype (Fig. 3) differs from the other specimens in the distinctly weaker development of the pseudocolumella and dissepimentarium. This is interpreted as intraspecific variation, though we can not exclude another decision in view of the restricted available material of only four specimens (but known from one locality in two directly neighbouring beds). The occurrence of the genus/species in other regions (especially Europe), where such small Rugosa of the cold and deep-water facies often remained unstudied, might be expected.

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#### 6. References

- Aitken, S. A., Collom, Ch. J., Henderson, Ch. M. & Johnston, P. A., 2002. Stratigraphy, palaeoecology, and origin of Lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco, Africa. Bulletin of Canadian Petroleum Geology 50, 217-243.
- Alberti, G. K. B., 1982. Der Hamar Laghdad (Tafilalt, SE Marokko), eine bedeutende Fundstätte devonischer Trilobiten. Natur und Museum, 112, 172-182.
- Belka, Z., 1998. Early Devonian Kess-Kess carbonate mud mounds of the eastern Anti-Atlas (Morocco), and their relation to submarine hydrothermal venting. Journal of Sedimentary Research 68: 368-377.
- Belka, Z. & Berkowski, B., 2005. Discovery of thermophilic corals in an ancient hydrothermal vent community, Devonian, Morocco. Acta Geologica Polonica, 55, 1-7.

- Berkowski, B., 2004. Monospecific rugosan assemblage from the Emsian hydrothermal vents of Morocco. Acta Palaeontologica Polonica, 49/1, 75-84.
- Berkowski, B., 2006. Vent and mound rugose coral associations from the Middle Devonian of Hamar Laghdad (Anti-Atlas, Morocco). Geobios, 39/2, 155-170.
- Berkowski, B., 2008. Emsian deep-water Rugosa assemblages of Hamar Laghdad (Devonian, Anti-Atlas, Morocco). Palaeontographica, Abteilung A 284/1-3, 17-68.
- Berkowski, B., 2012. Life strategies and function of dissepiments in rugose coral *Catactotoechus instabilis* from the Lower Devonian of Morocco. Acta Palaeontologica Polonica, 57/2, 391-400. (DOI: 10.4202/app.2010.0048).
- Berkowski, B. & Klug, C., 2012. Lucky rugose corals on crinoid stems: unusual examples of subepidermal epizoans from the Devonian of Morocco. Lethaia, 45, 24–33. (DOI: 10.1111/j.1502-3931.2011.00278.x).
- Brachert, T. C., Buggisch, W., Flügel, E., Huessner, H., Joachimski, M. M., Tourneur, F. & Walliser, O. H., 1992. Controls of mud mound formation: the Early Devonian Kess-Kess carbonates of the Hamar Laghdad, Antiatlas, Morocco. Geologische Rundschau, 81, 15-44.
- Cavalazzi, B., Barbieri, R. & Ori, G. G., 2007. Chemosynthetic microbialites in the Devonian carbonate mounds of Hamar Laghdad (Anti-Atlas, Morocco). Sedimentary Geology 200, 73-88.
- Fedorowski, J., 1974. The Upper Palaeozoic tetracoral genera Lophophyllidium and Timorphyllum. Palaeontology, 17/3, 441-473.
- Fedorowski, J., 1986. Permian Rugose Corals from Timor (remarks on Schouppé & Stacul's collections and publications from 1955 and 1959). Palaeontographica Abteilung A191/4-6, 173-227.
- Fedorowski, J., 2003. Podgromady [subclasses] Rugosa Milne Edwards et Haime, 1850, Dividocorallia Fedorowski, 1991. In Sarnecka, E. (ed.), Budowa geologiczna Polski. Tom III. Atlas skamieniałości przewodnich i charakterystycznych. Część 1b-z.1,z.2. Dewon. [Geological structure of Poland. Vol. III. Atlas of index and characteristic fossils. Part 1b, sheet 1-2. Devonian]. Państwowy Instytut Geologiczny, Warszawa, 49-124, 796-808. [in Polish].
- Fedorowski, J., 2009, Morphogenesis and taxonomic value of the circumaxial skeleton in Rugosa (Anthozoa). Lethaia, 42, 232-247.
- Fedorowski, J., 2010. Some peculiar rugose coral taxa from Upper Serpukhovian strata of the Czech Republic. Acta Geologica Polonica, 60/2, 165-198.
- Fedorowski, J. & Vassilyuk, N. P, 2011. Early Bashkirian Rugosa (Anthozoa) from the Donets Basin, Ukraine. Part 3. On the genera *Cyathaxonia* Michelin, 1847 and *Barytichisma* Moore and Jeffords, 1945. Acta Geologica Polonica 6/2, 133-152.
- Goryanov, V. B. & Klishevich, V. L., 1968. Les Tétracoralliaires et les Tentaculites des couches de passage Siluro-Dévonienne du sud Tien Chan. In Oswald, D. H. (ed.), International Symposium on the Devonian System, Calgary 1967, 2, Alberta Society of Petroleum Geologists, Calgary, 905-911 (dated 1967).
- Hill, D., 1938-1941. A monograph on the Carboniferous rugose corals of Scotland. The Palaeontographical Society [Monographs], London, 1-213.
- Hill, D., 1956. Rugosa, Heterocorallia. In Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata, Geological Society of America, New York, University of Kansas Press, F233-327.
- Hill, D., 1981. Rugosa and Tabulata. In Teichert, C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata, Supplement 1. Geological Society of America, Boulder, University of Kansas Press, 1-762.
- Hollard, H., 1974. Recherches sur la stratigraphie des formations du Dévonien moyen, de l'Emsien supérieur au Frasnien, dans le Sud du Tafilalt et dans le Ma'der (Anti–Atlas oriental). Notes et Mémoires du Service Géologique du Maroc, Rabat, 264, 7-68.
- Kato, M., 1963. Fine skeletal structures in Rugosa. Journal of the Faculty of Science, Hokkaido University, Sapporo, series IV, geology and mineralogy, 11/4, 571-630.
- Ludwig, R., 1865-1866. Corallen aus paläolithischen Formationen. Palaeontographica, 14/4-6, 133-244, 249-252.
- Massa, D., Combaz, A. & Manderscheid, G. 1965. Observations sur les séries Siluro–Dévoniennes des confins Algéro-Marocains du Sud. Notes et Mémoires, Compagnie Française des Pétroles 8, 1-187.
- Maurer, F., 1885. Die Fauna der Kalke von Waldgirmes bei Giessen. Abhandlungen der Hessischen Geologischen Landesanstalt, 1, 62-340.

- Milne-Edwards, H. & Haime, J., 1848a. Recherches sur les polypiers. Premier Mémoire: Observations sur la structure et le développement des polypiers en général. Annales des Sciences Naturelles, Paris, série 3, Zoologie, 9, 37-89.
- Milne-Edwards, H. & Haime, J., 1848b. Recherches sur les polypiers. 2.Monographie des Turbinolides. Annales des Sciences Naturelles, Paris, série 3, Zoologie, 9, 211-344.
- Milne-Edwards, H. & Haime, J., 1850-1855. A Monograph of the British Fossil Corals. The Palaeontographical Society [Monographs], London, I-LXXXV, 1-322.
- Milne-Edwards, H. & Haime, J., 1851. Monographie des Polypiers fossiles des terrains paléozoiques, précédée d'un tableau général de la classification des polypes. Archives du Muséum d'Histoire Naturelle, Paris, 5, 1-502.
- Mounji, D., Bourque, P.-A., & Savard, M. M., 1998. Hydrothermal origin of Devonian Conical Mounds (kess-kess) of Hamar-Lakhdad Ridge, Anti-Atlas, Morocco. Geology 26, 1123-1126.
- Opinion 946, International Commission of Zoological Nomenclature, 1971. Ludwig (R.), 1865-66, «Corallen aus paläolithischen Formationen» (Palaeontographica 14): suppressed under the plenary powers. Bulletin of Zoological Nomenclature, London, 27/5-6, 226.
- Peckmann, J., Walliser, O. H., Riegel, W. & Reitner, J., 1999. Signatures of hydrocarbon venting in a Middle Devonian carbonate mound (Hollard Mound) at the Hamar Laghdad (Antiatlas, Morocco). Facies, 40, 281-296.
- Peckmann, J, Little, CTS, Gill, F and Reitner, J., 2005. Worm tube fossils from the Hollard Mound hydrocarbon-seep deposit, Middle Devonian, Morocco: Paleozoic seep-related vestimentiferans? Palaeogeography, Palaeoclimatology, Palaeoecology, 227/1-3, 242 - 257.
- Roch, E. 1934., Sur des phénomènes remarquables observés dans la region d'Erfoud (confins algéro-marocains du Sud). Association Études de la Géologie Méditerranéenne Occidentale 5, 1-10.
- Różkowska, M., 1969. Famennian Tetracoralloid and Heterocoralloid fauna from the Holy Cross Mountains (Poland). Acta Palaeontologica Polonica, 14/1, 1-187.
- Schindewolf, O. H., 1942. Zur Kenntnis der Polycoelien und Plerophyllen. Eine Studie über den Bau der "Tetrakorallen" und ihre Beziehungen zu den Madreporarien. Abhandlungen des Reichsamts für Bodenforschung, Berlin, Neue Folge, 204, 1-324.
- Scrutton, C. T. 1971., Palaeozoic coral faunas from Venezuela, I. Silurian and Permo-Carboniferous corals from the Merida Andes. Bulletin of the British Museum (Natural History), Geology, 20/5, 183-227.
- Sutherland, P. K., 1965. Henryhouse Rugose Corals. Bulletin, Oklahoma Geological Survey, Norman, 109, 1-92.
- Volk, M., 1939. Das Oberdevon am Schwarzburger Sattel zwischen Südrandspalte und Kamm des Thüringer Waldes. Sitzungsberichte der physikalisch-medizinischen Sozietät, Erlangen, 70 (for 1938), 147-278.
- Weissermel, W., 1939. Die Korallen des thüringischen Devons. 1. Korallen aus Oberdevon im westlichen Schiefergebirge Thüringens. Jahrbuch der Preußischen Geologischen Landesanstalt, Berlin, 59, 353-369.
- Wendt, J., 1993. Steep-sided carbonate mud mounds in the Middle Devonian of the eastern Anti-Atlas, Morocco. Geological Magazine, 130, 69-83.
- Weyer, D., 1971. Famaxonia, ein neues Rugosa-Genus aus der Wocklumeria-Stufe (Oberdevon) des Thüringischen Schiefergebirges. Geologie, 20/9, 1025-1033.
- Weyer, D., 1980. Zur Kenntnis seltener Petraiidae (Anthozoa, Rugosa) aus dem amerikanischen Obersilur. Zeitschrift f
  ür Geologische Wissenschaften, 8/9, 1209-1216.
- Weyer, D., 1984. Korallen im Paläozoikum von Thüringen. Hallesches Jahrbuch für Geowissenschaften, 9, 5-33.
- Weyer, D., 2001. *Muenstraia*, ein neues Rugosa-Genus (Anthozoa) aus dem Obersilur und Unterdevon. Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, 4, 71-82.
- Weyer, D., 2004. Neue Rugosa-Funde aus dem Unter-Famenne von Deutschland (Anthozoa, Oberdevon). Geologisches Jahrbuch Hessen, 131, 203-223.
- Weyer, D., 2005. Antilacca, ein neues Rugosa-Genus aus dem mitteleuropäischen Unterdevon. Abhandlungen und Berichte, Museum f
  ür Naturkunde, Magdeburg, 28, 5-21.

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- Weyer, D., 2008. Revision des Ludwig/Kunth-Gesetzes zur Septeninsertion der Supraordo Rugosa (Anthozoa, Ordoviz—Perm). Abhandlungen und Berichte f
  ür Naturkunde (Museum f
  ür Naturkunde Magdeburg), 30, 85-14 (dated 2007).
- Weyer, D., Feist, R. & Girard, C. 2003. Conodonta, Trilobita, and Anthozoa near the Late Frasnian Upper Kellwasser Event of the Geipel Quarry section in Schleiz, Thuringian Mountains (Germany). Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, 6, 71-78.
- Weyer, D. & Zagora, K., 1990. Die ehemalige Givet-Fossilfundstelle Büchenberg im Unterharz. Hallesches Jahrbuch für Geowissenschaften, 15, 21-42.
- Wrzołek, T., 2002. Devonian history of diversity of the rugosan *Cyathaxonia* fauna. Acta Palaeontologica Polonica, 47/2, 397-404.
- Wu, Wang-shi & Liao, Wei-hua, 1988. Some Famennian Rugose Corals from Yishan, Guangxi. Acta Palaeontologica Sinica, 27/3, 269-277 (in Chinese).
- Yu Chien-Chang (Jian-Zhang), Lin Ying-Dang, Shi Yen, Huang Zhu-Xi & Yu Xue-guang, 1983. Carboniferous and Permian corals. Jilin Peoples Publishing House, Changchun, 1-357 [in Chinese].