Freiberger Forschungshefte, C 548	*psf* (22)	109 – 151	Freiberg, 2014

Thurispina nov. gen. (Anthozoa, Rugosa) from the Upper Famennian of Thuringia (Germany)

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with 20 figures

Weyer, D. (2014): *Thurispina* nov. gen. (Anthozoa, Rugosa) from the Upper Famennian of Thuringia (Germany). – *Paläontologie*, *Stratigraphie*, *Fazies* (22), Freiberger Forschungshefte, C 548: 109–151; Freiberg.

Keywords: trabicula, septal microstructure, non-trabicular trend, ontogenetic methods, Devonian, Upper Famennian, corals, Schwarzburg Anticline.

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Contents:

Abstract

Thurispina gen. nov. and its monotypic type species *Thurispina jogi* sp. nov. are described from the Upper Famennian (*Wocklumeria* Genozone). The coral occurs in the Bohlen section near Saalfeld (southeastern flank of the Schwarzburg Anticline) as a rare taxon of the ammonoid facies [with *Wocklumeria sphaeroides* (Richter, 1848)] or basinal entomozoid ostracod shale facies [with *Richterina striatula* (Richter, 1848), *Richterina costata* (Richter, 1869), and *Maternella hemisphaerica* (Richter, 1848)]. The new genus of the suborder Plerophyllina Sokolov, 1960 is classified with a diagnosis “Pentaphyllidae with trabicular septal microstructure” in a not yet phylogenetically redefined subfamily Anisophyllinae Ivanovskiy, 1965 (family Plerophyllidae Koker, 1924 / Pentaphyllidae Schindewolf, 1942), together with *Anisophyllum* Milne-Edwards & Haime, 1850 (Ludlow), *Oligophyllum* Počta, 1902 (Ludlow–Upper Emsian) und *Pentaxon* Glinski, 1999 (Givetian). This touches several, sometimes controversially discussed problems of skeleton morphology (septal microstructure, interpretation of ontogeny in series of cross sections) and taxonomy.

A redefinition of the morphological term trabicula, introduced by Milne-Edwards & Haime (1848, 1850 – “poutrelles” or spines of septal margins) for Scleractinia and Tabulata, misnamed trabecula by Pratz (1882), accepted for the Palaeozoic Rugosa by Hill (1935), uses as a morpho-terminological type the Silurian *Palaeocyclus porpita* (Linné, 1767). When Schindewolf (1942) could not find trabiculae in his Carboniferous–Permian Plerophyllina collections, he proposed a second type of septal microstructure called lamellar; in spite of his priority, the name fibro-normal (Kato, 1963) is preferred because of ambiguity (since Koker, 1924) with the meaning of “lamellar”.

Suborder diagnoses like “Zaphrentoidina = Rugosa with lamellar septal microstructure” (Schouppé & Stacul, 1959) were accepted or refused (mainly by Iljina and Fedorowski, who everywhere observed only trabiculae) – however, both structures exist mainly in the ahermatypic suborders Cyathaxoniina, Zaphrentoidina, and Plerophyllina. There, the older plesiomorph trabicular microstructure repeatedly changes towards the younger apomorph fibro-normal one along independent phylogenetical lines (obviously with transitions). This is here named the non-trabicular trend (*sensu* LANG 1923), already distinctly described by KATO (1963); perhaps even MILNE-EDWARDS (1857) had similar ideas for Scleractinia.

A practicable boundary between trabicular septa (spinous margins) and fibro-normal septa (smooth margins) requires a definition of "smooth" – proposed is a polished glossy limestone surface (already used in the times of MILNE-EDWARDS & HAIME), feasible with grinding powder of 0,5–5 µm. Thus, the minimal diameter of spines at distal septal margins should be 10 µm (minitrabiculae in Scleractinia – RONIEWICZ, 1984). When traceability of trabiculae is difficult in subtabular thin sections due to diagenetic recrystallisations, other methods to see them as spines can be applied (study of uncorroded calices or of tangential longitudinal sections in the upper calice). Half-moon-shaped growth segments ("Stirnzonen" – SCHOUPPÉ & STACUL, 1955), seen in cross sections of many Carboniferous–Permian ahermatypic Rugosa are accepted as primary biogenic structures in fibro-normal septa, against the opposite interpretation as secondary diagenetic (with relics of trabiculae), often proclaimed since FEDOROWSKI (1974). Such septa have no thin filiform dark line ("Urseptum"), but started their growth with a broadly rounded front already at the upper calicular rim.

Zusammenfassung

Aus dem obersten Famenne (*Wocklumeria*-Genozone) werden *Thurispina* nov. gen. und ihre vorerst einzige Art *Thurispina jogi* n. sp. beschrieben. Die neue Gattung kommt selten in der Cephalopoden-Fazies – mit *Wocklumeria sphaeroides* (RICHTER, 1848) – beziehungsweise Cypridinen-Schiefer-Fazies – mit *Richterina striatula* (RICHTER, 1848), *Richterina costata* (RICHTER, 1869) und *Maternella hemisphaerica* (RICHTER, 1848) – des bekannten Bohlen-Profils bei Saalfeld an der SE-Flanke des Schwarzburg-Antiklinoriums vor. Das Taxon der Subordo Plerophyllina SOKOLOV, 1960 wird zusammen mit *Anisophyllum* MILNE-EDWARDS & HAIME, 1850 (Ludlow), *Oligophyllum* POČTA, 1902 (Ludlow–Oberems) und *Pentaxon* GLINSKI, 1999 (Givet) in eine redefinierte, leider noch nicht phylogenetisch (kladistisch) fassbare Subfamilia Anisophyllinae IVANOVSKIY, 1965 der Familia Plerophyllidae KOKER, 1924 / Pentaphyllidae SCHINDEWOLF, 1942 klassifiziert mit der Diagnose „Pentaphyllidae mit trabiculärer Septenmikrostruktur". Damit sind traditionelle, mitunter schon kontrovers diskutierte Vorstellungen zur Morphologie (Septenmikrostruktur, Ontogenie-Interpretation in Querschliffserien) und Taxonomie in Frage gestellt.

Für die paläozoische Supraordo Rugosa war der morphologische Terminus „Trabecula" (PRATZ, 1882), korrekt Trabicula (MILNE-EDWARDS & HAIME, 1848, 1850 – „poutrelles" oder Septalrandspinae) besser zu definieren und durch einen morpho-terminologischen Typus *Palaeocyclus porpita* (LINNÉ, 1767) zu fixieren. SCHINDEWOLF (1942) hatte in Plerophyllina des Karbon–Perm keine Trabiculae gefunden, sondern einen zweiten Grundtyp der Septenmikrostruktur entdeckt, den er „lamellär" nannte; weil diese Bezeichnung mehrdeutig ist und von KOKER (1924) in einem ganz anderen Sinne verwendet wurde, sollte heute besser der Terminus „fibro-normal" (KATO, 1963) gebraucht werden. Danach waren Subordo-Definitionen wie „Zaphrentoidina = Rugosa mit lamellärer Septenmikrostruktur" (SCHOUPPÉ & STACUL, 1959) entstanden, die überall Trabiculae wahrnehmende Kritiker (ILJINA, FEDOROWSKI) ablehnten. Hauptsächlich in den ahermatypischen Rugosa-Unterordnungen Cyathaxoniina, Zaphrentoidina und Plerophyllina existieren jedoch beide Baupläne – die ältere plesiomorphe trabiculäre Septenmikrostruktur wird wiederholt in unabhängigen Entwicklungslinien durch die apomorphe fibro-normale Septenmikrostruktur ersetzt, wobei offenbar Übergänge vorkommen. Im Sinne von LANG (1923) wird dies hier als der non-trabiculäre Trend bezeichnet, den KATO (1963) bereits klar beschrieb und nur noch nicht benannte; vermutlich hatte schon MILNE-EDWARDS (1857) ähnliche Vorstellungen für Scleractinia.

Eine praktikable Grenze zwischen trabiculärer (spinöse Septenränder) und fibro-normaler Septenmikrostruktur (glattrandige Septen) erfordert die Definition von „glatt": Das soll eine polierte glänzende Kalkstein-Oberfläche sein, die mit Schleifpulver von 0,5–5 µm herstellbar ist. Septalrandspinae müssen dann mindestens 10 µm Durchmesser besitzen, wie bei den Minitrabiculae der Scleractinia (RONIEWICZ, 1984). Weil sich die Existenz von Trabiculae in subtabularen Dünnschliffen oft wegen diagenetischer Rekristallisationen kaum beweisen lässt, sollten auch andere Methoden zum Nachweis der Septalrand-Spinae dienen (Studium freier Kelche, caliculare tangentiale Längsschliffe). In Querschliffen vieler ahermatypischer Rugosa des Karbon–Perm zu beobachtende „Stirnzonen" (SCHOUPPÉ & STACUL, 1955) – Halbmond-artige, oft Sichel-förmige Anwachssegmente der Septen – werden als eindeutig primär biogen fibro-normal interpretiert, nicht (wie so oft seit FEDOROWSKI, 1974) als sekundär diagenetisch mit Trabicula-Relikten.

Ontogenetische Studien solitärer Rugosa untersuchen konventionell subtabulare Querschliffserien (möglichst bis zur äußersten Polyparspitze); diese sekundäre Postcalyx-Ontogenie zeigt aber nur die Abfolge von vollendeten Kelchbasis-Bildern. Wie diese vorher gewachsen sind, kann aus der primären Calyx-Ontogenie (*sensu* WEYER, 2005) abgeleitet werden: sie analysiert Querschliffserien vom Kelchoberrand bis zur Kelchbasis, denn jedes beliebige Querschliffstadium entstand zuerst an einem Kelchoberrand.

1 Introduction

The discovery of the new genus to be described here is connected with three controversially discussed morphological problems mainly of the Rugosa suborder Plerophyllina SOKOLOV, 1960 (Ludlow—Changhsingian). The first open question is the absence of "trabeculae", postulated with good reasons by SCHINDEWOLF (1942), later opposed by ILJINA (1965–1986) or FEDOROWSKI (1974–2012). Thus, the common morphological glossary of HILL (1981) needs a redefinition of its term "trabecula". The second uncertainty exists in the taxonomical evaluation of four, five, or six prominent, often rhopaloid protosepta in some members of that suborder, as proposed recently for the genus *Pentaphyllum* DE KONINCK, 1872 (FEDOROWSKI 2009a). The third problem concerns methods how to study ontogeny in Rugosa.

Studied Rugosa are stored in the following institutions: 1 – Museum of Natural History (Leibniz Institute) at Humboldt University, Berlin (MB); 2 – Bundesanstalt für Geologie und Rohstoffe, Berlin department (BGR); 3 – Geological Institute, Technical University Bergakademie Freiberg (FG, BA Freiberg); 4 – Palaeontological Institute, Russian Academy of Sciences, Moscow (PIN Moskva). Abbreviations: CS cross section, LS longitudinal section, TS thin section, P peel, R remaining piece.

In 2011, the first of these institutions received the famous "Johannes-Wanner-coral-collection" (Permian of Timor island, Indonesia), transferred by order of Prof. Dr. KLEMENS OEKENTORP (chief of the Forschungsstelle für Korallenpaläozoologie, founded in 1964 at the Geologisch-Paläontologisches Institut, Westfälische Wilhelms-Universität Münster) from that institute to Berlin. Originally, the coral fauna was in the hands of FRANZ HERITSCH (1882–1945) in Graz, where one of his students studied the Tabulata (HEHENWARTER, 1951); this material was given back to JOHANNES WANNER in Bonn and is now stored there at the Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Rheinische Friedrich-Wilhelms-Universität. In 1953 the Rugosa collection from Timor was rendered to another student of HERITSCH, ALEXANDER VON SCHOUPPÉ (1915–2004), who worked since 1953 in Münster. Here the main morphological and taxonomical studies were published: SCHOUPPÉ (1955, 1956, 1957a, 1957b), SCHOUPPÉ & STACUL (1955, 1959a, 1959b, 1961, 1962, 1966), OEKENTORP (1972, 1974a, 1974b, 1980, 1984, 1989, 2001), NIERMANN (1975), SORAUF (1978, 1983, 1984), SORAUF & FREIWALD (2002), FEDOROWSKI (1986). The collection is now catalogued step by step in the electronic data base of the Museum of Natural History (Leibniz Institute) at Humboldt University in Berlin.

2 The morphological term "trabicula"

Unexpectedly, the new genus proposed here has well developed "trabeculae" or distinctly spinous distal septal margins. This feature contradicts the opinions of SCHINDEWOLF (1942: his family "Polycoeliidae", now suborder Plerophyllina, characterized by the lamellar microstructure) and SCHOUPPÉ & STACUL (1959: their new suborder Zaphrentoidina, which included the later named Plerophyllina, was diagnosed as "Pterocorallia mit lamellärer Septenstruktur"), but seems to correspond to the interpretations of ILJINA (1965, 1980, 1986) and FEDOROWSKI (1974, 2012). The reality says: both microstructures (plesiomorph = "trabecular", apomorph = lamellar) exist within the Plerophyllina, as also in further suborders – there is a common trend (*sensu* LANG, 1923, 1938), already clearly indicated by KATO (1963), here described below as the "non-trabicular trend" in the superorder Rugosa.

2.1 History

In 1848, the term poutrelle = trabiculina (= trabicula of 1850) concerned only Scleractinian corals, there characterizing three types of septa:

1. The main illustration (MILNE-EDWARDS & HAIME, 1848: 62, pl. 5/1b – the only one directly explained as "poutrelles cloisonnaires") shows *Alveopora fenestrata* (LAMARCK, 1816) with "poutrelles styliformes", as an example for septa appearing as rows of big and well separated spines (fig. 1).
2. *Coscinastraea bottae* MILNE-EDWARDS & HAIME, 1848 = *Coscinaraea monile* (FORSKÅL, 1775) was figured (1848: 62, pl. 5/2b) for porous compact septa looking like trellis-work. *Turbinolia elliptica* BRONGNIART in CUVIER & BRONGNIART, 1822 was mentioned (1848: 62) for cribriform septa; they occur also in Rugosa (fig. 2).
3. Massive aporous septa as in Cyathinae (= Caryophylliidae) still demonstrate the course of the poutrelles by the orientation of tubercles and granulae on their septal flanks (1848: 62, pl. 4/2a,3a, examples *Turbinolia dixonii* MILNE-EDWARDS & HAIME, 1848 and *Flabellum gallapagense* MILNE-EDWARDS & HAIME, 1848) and by a spinose septal margin (MILNE-EDWARDS, 1857: 32).

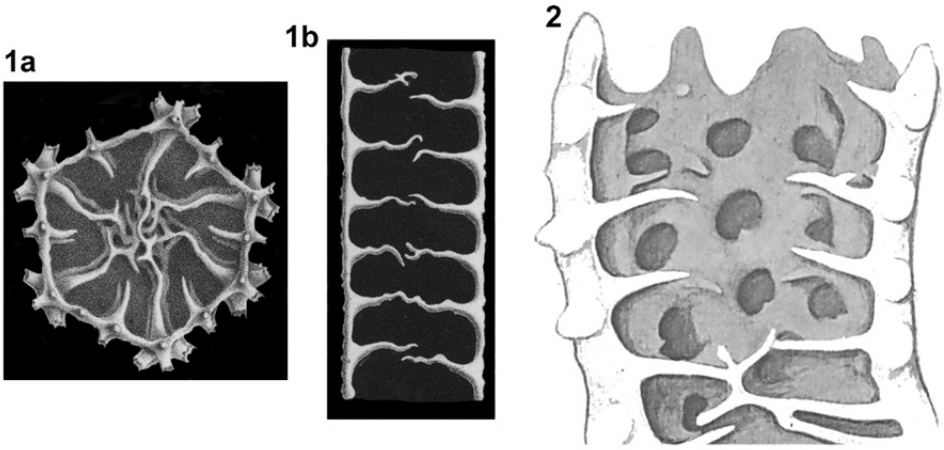


Fig. 1: Trabiculae (*sensu* Milne-Edwards & Haime, 1848) or fascicular = stylophyllid microstructure (*sensu* Roniewicz & Morycowa, 1993: 233): widely spaced long septal spines in *Alveopora fenestrata* (Lamarck, 1816), rezent, Indopazifik (without locality data). 1a , b – copied from Milne-Edwards & Haime (1848: pl. 5/1a, 1b, poutrelles cloisonnaires = styliformes in broken corallites of *Pocillopora fenestrata*, “magnified”).

2 – copied from Koch (1896: pl. 1/7, *Alveopora retusa* Verrill, 1864, x 30); according to Veron & Pichon (1982: 110, 121) a junior synonym of *Alveopora fenestrata*.

This genus could be one of the candidates for the Scleractinian morphotype of the term trabicula because of the suitable illustration in 1848, but there are doubts whether it represents the plesiomorph Triassic type of the Stylophyllidae Volz, 1896 or an apomorph, secondarily simplified Cenozoic septal structure. The problem has increased since the genetic investigation of Romano & Cairns (2000: 1054, 1062): *Alveopora* Blainville, 1830 is no longer a member of Poritidae Gray, 1842, but it was transferred to Acroporidae Verrill, 1902.

Later (1850–1855, 1851), the term was also used by them for Tabulata (*Halysites*, *Heliolites*, *Favosites*, *Pleurodictyum*), but never for Rugosa (1851: 160 – “les cloisons … ne sont jamais poreuses, ni poutrellaires”).

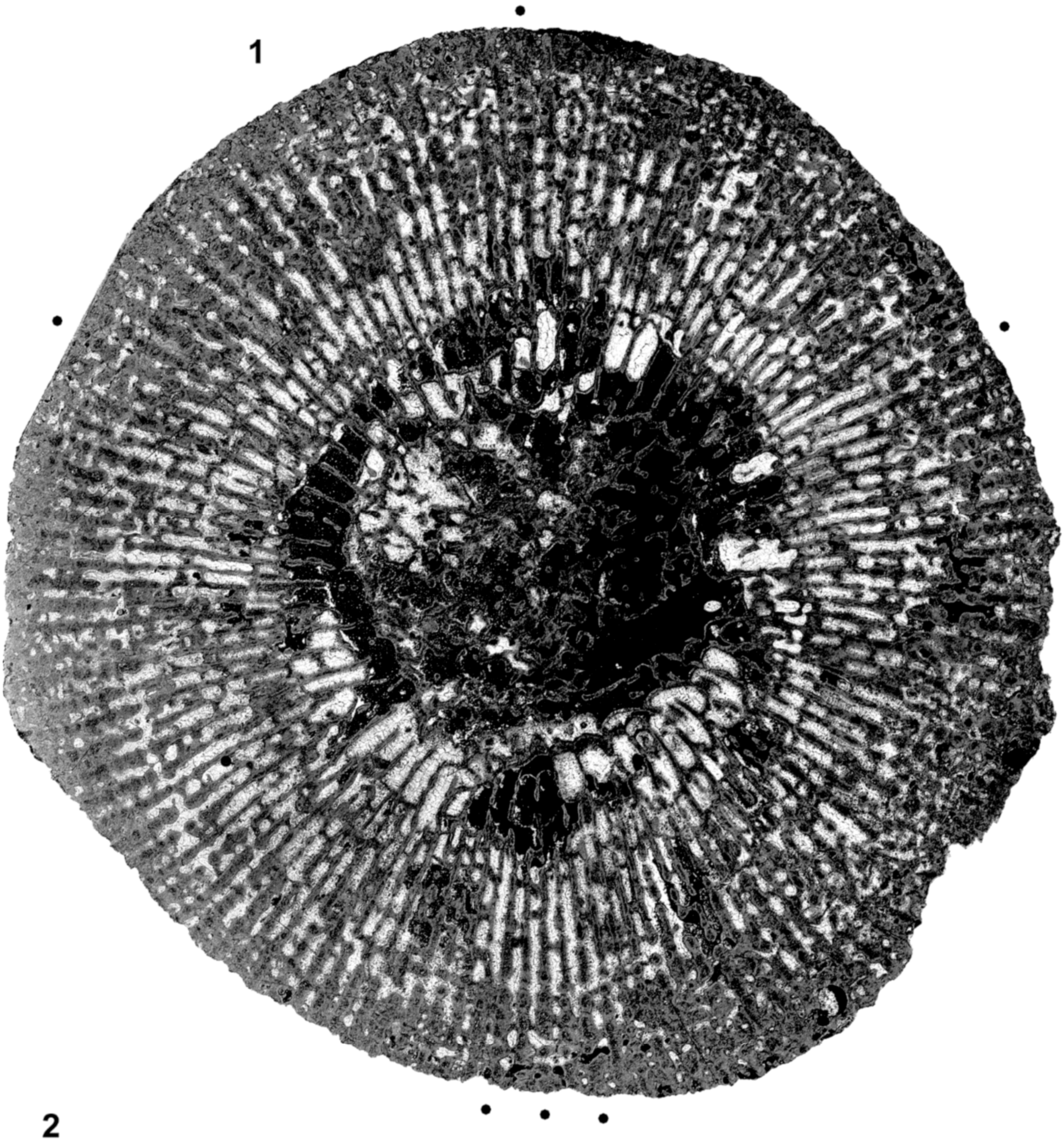
4. Milne-Edwards (1857: 32) added a fourth type of Scleractinian septa, which seems worth to be cited in his own words: “mais l’espèce d’ossification dont dépend la formation des parties dures peut s’opérer aussi d’une manière très-complète, à ce point que l’on ne puisse plus reconnaître dans les lames calcaires ni dentelures marginales, ni grains latéraux, aucune trace en un mot des elements primitives don’t elles sont formées (exemple: *Desmophyllum*).”

This might allow an interpretation as first observation of the non-trabicular septal microstructure (lamellar *sensu* Schindewolf, 1942, fibro-normal *sensu* Kato, 1963), discerned by its smooth distal margins. Perhaps, in 1857 Milne-Edwards had already – two years before the classical publication of Darwin – some unexpressed ideas on Scleractinia about evolution along the here named non-trabicular phylogenetic trend (well described for Rugosa by Kato, 1963); and surprisingly he knew the correct plesiomorph → apomorph direction (in contradiction to Schindewolf, 1942: 28, who proposed the incorrect opposite development lamellar → trabicular).

Fig. 2: Trabiculae in *Calostylis* sp. nov., Late Wenlock, Ninase Formation of upper Jaani Stage, Suurikupank cliff near Undva village, northwestern Saaremaa island, Estonia, coll. D. Weyer, 1996. No. MB.K.7947.

1 – cross section at calicular base, x 4.5, with septal pores and synapticulae. 2 – subtabular median longitudinal section (right-angled to cardinal-antiseptal plane), x 4, everted calice with strongly porous septa of rather incompletely fused trabiculae (in Scleractinia called cribriform by Milne-Edwards & Haime, 1848: 62).

1



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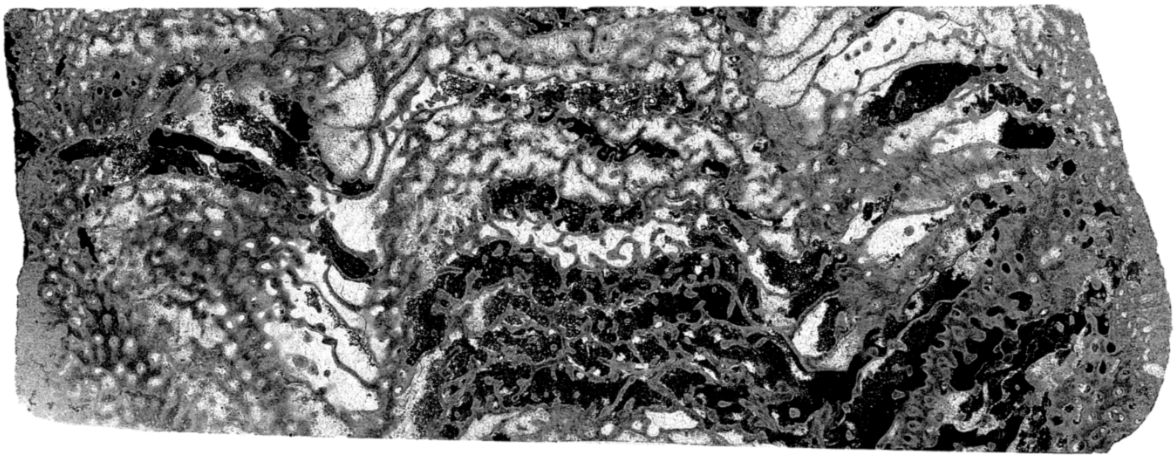


Perhaps, the example *Desmophyllum* EHRENBERG, 1834 might be cancelled as an intermediate between trabicular and lamellar septal microstructure. Modern scanning electron microscope studies (SORAUF & JELL, 1977: pl. 4/2) – though speaking of "smooth and rounded exsert septa in the calice" – proved the presence of very small trabiculae (diameter ca. 15–20 µm = minitrabiculae sensu RONIEWICZ & MORYCOWA, 1993) at least in some (but not necessarily in all) septa, and of course unvisible to MILNE-EDWARDS (1857). But, there exist really smooth septal margins without trabicular spines in many Rugosa (see SCHINDEWOLF, 1942).

The original use of the term trabicula in the publications of MILNE-EDWARDS & HAIME (1848, 1850–1855, 1851) and MILNE-EDWARDS (1857–1860) is ambiguous, but prefers septal structures. This was well analysed by HILL (1935: 499–501); she had written:

> "The following are instances of Edwards and Haime's use of the word trabecula and its derivatives. 'The septa cease to grow in a regular manner' near the axis 'and divide into a multitude of ramuscules or trabeculae (trabeculina), which grow more or less in a centripetal direction, subdivide, and fuse wherever they touch', forming a spongy or parietal columella (1848: p. 79, transl.) [= Axialsynapticulae of WEYER, 1972: 711]. In 1850 they used the form trabicula, with adjective trabicular, for at least eight different structures, but always for rods or plates helping to form a network. Thus, p. V for trabeculina, p. VI for synapticula, p. XXXVI for processes uniting the inner edges of the septa to a lamellar columella in Astraeids, p. LV for the styliform processes of the septa of the Poritidae, p. LVI for the irregular rods and plates forming the cribriform septa of *Holarea*, p.123 for the regular rods forming the cribriform septa of *Microsolena*, p. 251 for the transverse and vertical plates of the coenenchyme of *Heliolites*, and p. 271 for the acanthine septa of *Halysites catenularia*."

Her clear words (1935: p. 499) to define the term trabecula should also be cited:

> "The fibres of which the septum is composed are grouped together to form spines, from the axes of which they radiate upwards. These spines are the TRABECULAE of Pratz, Ogilvie, and Vaughan, or 'poutrelles' (Edwards & Haime, 1848, p. 56). … Pratz (1882, p. 88) … adopted the term trabecula for the poutrelle, thus restricting in meaning a term which is usually general. In this he was followed by Ogilvie (1897, p. 124), Vaughan (1900, p. 39), and Bernard (1905, p. 13). Since the use of trabecula for 'poutrelle' has become so confirmed in descriptions of Hexacorals that it can hardly now be discontinued, it is here adopted for Rugose corals also."

For their coral studies (1848–1860), MILNE-EDWARDS and HAIME disposed only of the rather poor optical tools in the mid-19th century: pocket-lens, weak microscope. They analysed complete coral skeletons with well-preserved calices, transversely and longitudinally broken specimens, and polished surfaces. A pioneer in studying weathered casts offering interior features was LUDWIG (1812–1880; in his unfairly depreciated monograph of 1865/1866). The revolutionary introduction of the mineralogical thin section techniques into coral palaeontology/zoology started in Germany (KÖLLIKER, 1866; KUNTH ,1869; FISCHER-BENZON, 1871), not in Scotland (NICHOLSON, 1876), as indicated by BENTON (1979). Pioneers of microstructural research in corals were PRATZ (1882), KOCH (1882), VOLZ (1896), and especially OGILVIE (1897), followed by many subsequent studies (here to mention among this multitude only HILL, 1936; SCHINDEWOLF, 1942; WANG, 1950; KATO, 1963; RONIEWICZ & MORYZOWA, 1989). Further decisive impulses rose with the scanning electron microscopy, by the use of ultra-thin polished thin sections (LAFUSTE, 1970), and by consideration of diagenetic alterations within the calcareous skeleton (SORAUF, 1981; OEKENTORP, 2001). Unfortunately, this caused some neglecting of direct microstructural observations on skeleton surfaces in coral calices (with only few exceptions as CHEVALIER, 1961 or GILL, 1977).

The size of trabiculae is now measured mostly in thin sections (both cross and longitudinal) and varies within broad limits, partly according to the size of corals or corallites, but often also as a diagnostic feature in taxonomical units. Well-preserved free calices of recent and Tertiary Scleractinia were also be used for measurements along the distal septal margins without any sectioning. VAUGHAN (1900) reported trabicular diameters of 16–830 µm. RONIEWICZ (1989: 8) and RONIEWICZ & MORYCOWA (1993) differentiated between mini-trabiculae (20–50 µm) and thick-trabecular (macro-trabiculae, 50–300 µm). An adult specimen of one of the Estonian cow-horn like corals (genus *Kenophyllum* DYBOWSKI, 1873, Upper Ordovician, Bolindian, Ashgillian Pirgu Stage) achieves trabicular diameters up to 1000 µm (fig. 3).

The precise coordination of internal septal microstructure and external spinose shape of the distal septal margin in Scleractinia and Rugosa was well known since MILNE-EDWARDS & HAIME (1848) and MILNE-EDWARDS (1857), and incontestably accepted by all later authors (e.g. PRATZ, 1882: 89 etc.; VOLZ, 1896: 7; HILL, 1935). KATO (1963: 582) summarized: "The differentiation of skeletal elements comes solely from the different modes of folding or invagination of basal ectoderm". Non-trabicular septa are the result of "spherulitic crystallization under linear control, the line being the crest of the septal invagination; this is in contrast to trabecular growth resulting from control by a number of separated points along the crest" (HILL, 1956: F236).

As original microstructures are often partially or totally destroyed during diagenesis (especially in Scleractinia when aragonite is transformed into calcite), it might be better to prove the presence or absence of trabiculae by looking for the micro-ornament of the septal margins into the calices. They are rarely available in Palaeozoic

Rugosa, but sometimes well studied (Sutherland, 1965: pls. 20/4b, 24/5b, 34/5; Plusquellec & Semenoff-Tian-Chansky, 1973). Preservation as natural cast (Steinkern) allows direct observation (Ludwig, 1865: pl. 40/1, 42/2, 46/1) or by latex/resine plastercast (Weyer, 1975: pls. 1–2). Sometimes, an artificial cast prepared with acetic acid is possible (here in *Thurispina,* see fig. 20/6). In cases of clay sediment filling the calcite calice, fluor acetic worked successfully to get free insight (Weyer, 1971a: pl. 6/1 – coarse trabiculae in *Neaxon*; 1978a: pl. 8/6–8 – fibro-normal septa in *Thecaxon*). Often, tangential longitudinal sections parallel to the interior margins of major septa will give sufficient results (as here for *Oligophyllum*: figs. 8–10). Such calicular observations concerning either trabicular or fibro-normal microstructures avoid diagenetic alterations which are more common in subtabular coral regions with sparite filling; normally, diagenesis did not change the calicular imprint of the ectoderm.

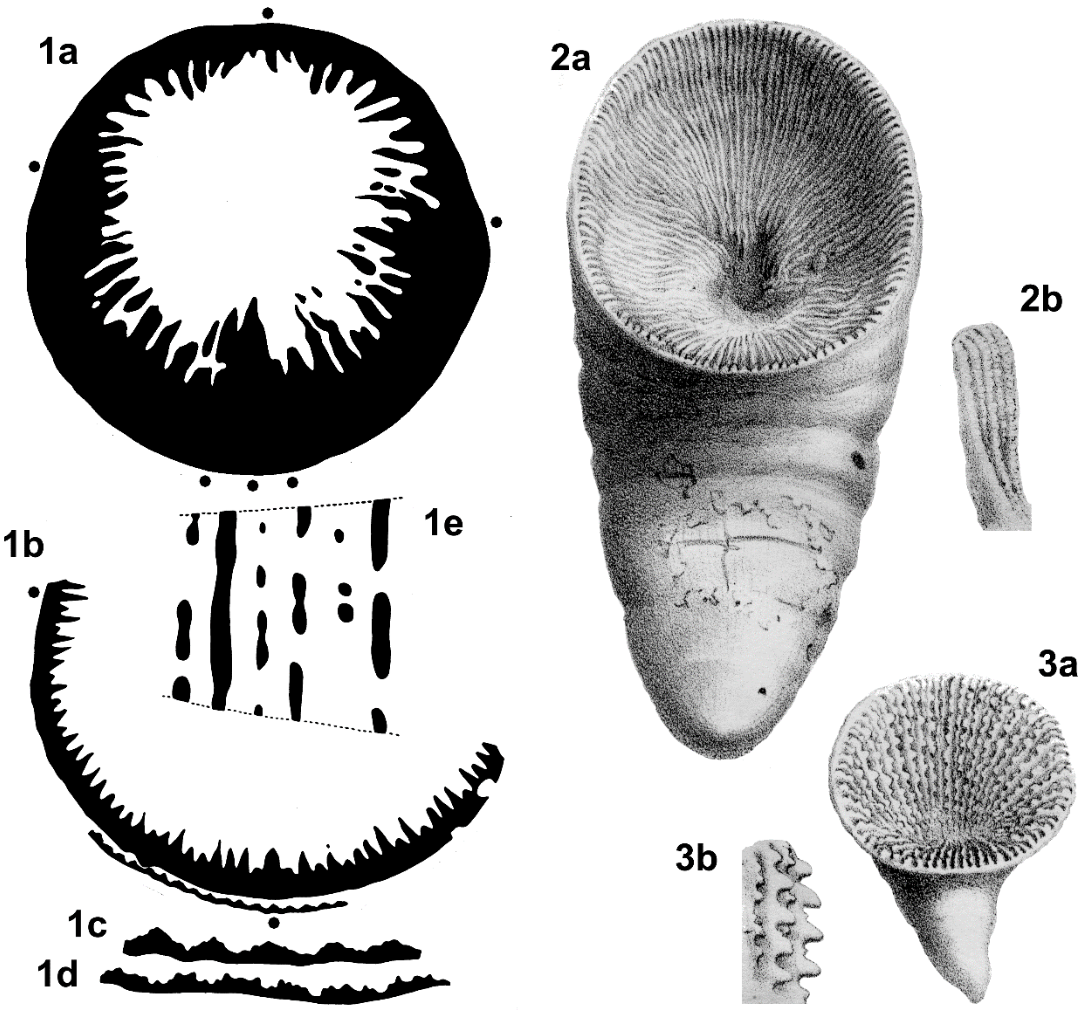


Fig. 3: Trabiculae of the Estonian Upper Ordovician genus *Kenophyllum* Dybowski, 1873. 1 – *Kenophyllum tenuilamellatum* (Eichwald, 1856), Vormsi Stage (F1b), Mõnuste (18 km S of Keila), coll. D. L. Kaljo 1954, no. MB.K.104, (duplicate peels in the Geological Institute, University Tallinn), a “cow-horn coral” (junior synonym: *Kenophyllum subcylindricum* Dybowski, 1873). (a) middle calicular cross section (no. 9), x 1.75; (b). upper calicular cross section (no. 13), x 1.75; (c) multitrabicular = rhabdacanth septa ear the upper calicular margin (cross section no. 13), x 6; (d) rhabdacanth septal detail at the uppermost preserved calicular margin (cross section no. 14), x 6; (e) monacanth trabicular spines in the upper calice (longitudinal section no. 1), x 5. 2 – *Kenophyllum tenuilamellatum* (Eichwald, 1856), lectotype (Geological Institute, State University, St.-Peterburg), copied from Eichwald (1860: 522, pl. 29/3), probably Pirgu Stage, Pühalepa (Hiiumaa island). (a) specimen with free calice, x 1; (b) septal margins with monacanth trabicular spines, magnified. 3 – *Kenophyllum dilatatum* (Eichwald, 1856), lectotype (Geological Institute, State University, St.-Peterburg), copied from Eichwald (1860: 522, pl. 29/2, junior synonym: *Petraia silurica* Dybowski, 1873), probably Vormsi Stage, Hohenholm near Körgessaare (Hiiumaa island). (a) specimen with free calice, x 1; (b) septal margins with monacanth trabicular spines, magnified.

The existence of non-trabicular septa seems to be quite uncommon among Scleractinia. It was indicated by PRATZ (1882) for the Rhaetian *Astraeomorpha* REUSS, 1854 with smooth septal margins; finally he named one septum entering two or three corallites as only one trabicula, but such an abuse of this term cannot be accepted. In 2014, EWA RONIEWICZ told me that Carnian *Astraeomorpha* have well inividualized trabiculae in contrast to Rhaetian representatives with only rarely developed trabiculae – this might indicate a transition from trabicular to fibro-normal microstructure even within one genus; earlier (RONIEWICZ, 1984) she had spoken of a non-trabicular structure in *Astraeomorpha*.

SCHINDEWOLF (1942: 27, fig. 6) found non-trabicular Rugosa and proposed for them the term “lamellar” microstructure (in German: lamellär). In spite of his priority, here the term “fibro-normal” (KATO, 1963: 604, including his fibro-lamellar or clathrate and his lamellar types) is preferred, because since KOKER (1924) the word “lamellar” was ambiguously used (RODRIGUEZ, 1989), over-emphasizing growth lamellation instead of growth direction of the calcareous fibres (perpendicular to the ectodermal secreting surface of the soft part).

2.2 Definition

The two basic types of coral septal microstructures (trabicular, fibro-normal) are explained in detail by SCHINDEWOLF (1942) and SCHOUPPÉ & STACUL (1966). They have been characterized as completely or decisive different (in German: “durchgreifend”, a vocable favoured by the first author). On the other hand, phyletic transitions have been discussed (SCHINDEWOLF, 1942: 25, 27, 28 – “diffuso-trabicular”). Following the old HERAKLIT wisdom “πάντα ρεί“, of course there exist continuous transitions: repeatedly the fibro-normal type had evolved from the trabicular type. Nevertheless, a dialectic view demands practicable boundaries, as for structure (naked eye – millimetre), microstructure (light microscope – micrometre), and nanostructure or ultrastructure (electron microscope – nanometre). Thus, the unprecise term “smooth” for a fibro-normal septal margin must be defined; I propose a polished glossy limestone surface (already used by our pioneers MILNE-EDWARDS and HAIME), which is achieved by grinding powder around 1 µm (0.5–5 µm). fig. 4 presents the example of such an uncorroded smooth septal margin. Then the size of trabicular spines or any discrimination of trabiculae starts with a diameter of >10 µm (as in minitrabeculae of RONIEWICZ, 1984, 1989; RONIEWICZ & MORYCOWA, 1989, 1993: 10–20–50 µm).

Usually, morphological terms are verbally defined, but, it is commendable to select in addition a species as “morpho-terminological type” in order to avoid deviating or ambiguous interpretations. Sometimes this had already be done (in part subsequently) for the glossary of the Anthozoan supraordo Rugosa: WEYER (1975: 25 – epitheca of MILNE-EDWARDS & HAIME, 1848, archaeotheca of ALLOITEAU, 1952; 1978a: 310 – lateral cardinal fossula; 1980b: 59, 61 and 1997: 38, 39 – new terms diploseptum and hyposeptum; 2008: 110 – different septa), FEDOROWSKI (2009b: 235, 238 – aulos of SMITH, 1928, new term circulotheca), BERKOWSKI & WEYER (2012: 247 – columella of EHRENBERG, 1834, pseudocolumella of MILNE-EDWARDS & HAIME, 1848).

In the case of “circulotheca”, its author indicated only a typical development in the genera *Syringaxon* LINDSTRÖM, 1882 and *Neaxon* KULLMANN, 1965. His illustrated Devonian (Upper Eifelian) “*Syringaxon*” (FEDOROWSKI, 2009b: figs. 4, 5) are typical members of *Laccophyllum* SIMPSON, 1900, which was obviously treated as a junior synonym of *Syringaxon* (following BERKOWSKI, 2008). For the moment, the only known holotype of the Silurian (Ludlow) type species *Syringaxon siluriensis* (MCCOY, 1850), revised by SUTHERLAND (1970), shows diplosepta as in the Sutherlandiniinae WEYER, 1972; it is better regarded as a *nomen dubium* waiting for a redescription based on additional records from the type locality. The alternative view – pathological specimen – of BERKOWSKI (2008: 39) seems less probable. Indeed, the term circulotheca needs and deserves a well-defined and abundantly found species as a morpho-terminological type – among the two genera proposed by FEDOROWSKI, here I select the Late Famennian *Neaxon regulus* (RICHTER, 1848) (see KORN & WEYER, 2003: 104, fig. 19).

Following HILL (1935, 1936) in adopting the term trabicula also for Rugosa, the morpho-terminological type is selected here among her studied “acanthine” taxa: *Palaeocyclus porpita* (LINNÉ, 1767) from the Silurian (top Llandovery – basal Wenlock, Telychian–Sheinwoodian, mostly Lower Visby Marls of Gotland, Sweden), a very common species (SCRUTTON, 1996). Likewise, this taxon is accepted as the type for the special mode of monacanth trabiculae (HILL, 1936).

A similar choice for Scleractinia should be done by experts of this supraordo. Temporarily I preferred the recent *Alveopora fenestrata* (LAMARCK, 1816), illustrated by MILNE-EDWARDS & HAIME (1848) as the probably most primitive and clearly trabicular septal type (fig. 1), but meanwhile (RONIEWICZ & MORYCOWA, 1993: 233) proposed to represent a non-trabicular microstructure (stylophyllid = fascicular).

On this occasion, a morpho-terminological type is selected for the term axialsynapticulae (still omitted in WEYER, 1972: 711, 1974: 161). They were among the Scleractinian trabiculae of MILNE-EDWARDS & HAIME (1848) and characterize many Rugosa of the Streptelasmatidae NICHOLSON, 1889 – there named “axial lobes” (HILL, 1956: F268) or “vermiform lobes on axial edges of septa” (HILL, 1981: F148). Examples are genera with a pseudocolumella (*Dalmanophyllum* LANG & SMITH, 1939) and without an axial boss (*Rhegmaphyllum* WEDEKIND, 1927); *Ditoecholasma* SIMPSON, 1900 and *Enterolasma* SIMPSON, 1900 offer an ideal pattern. *Enterolasma strictum* (HALL, 1874) from the Lower Devonian (Lochkovian, Helderbergian, New York) is proposed as the morpho-terminological type (SIMPSON, 1900: 203, figs. 11–12).

2.3 Half-moon shaped growth segments ("Stirnzonen")

Until today, this septal structure (well illustrated in SCHINDEWOLF, 1942: pl. 7/1b, 11/1, 13/4b, and named by SCHOUPPÉ & STACUL, 1955, 1966) is interpreted either biogenic or diagenetic, as fibro-normal or as trabicular. It is typical in mainly Plerophyllina and for many ahermatypic taxa of the famous Permian Rugosa of Timor island.

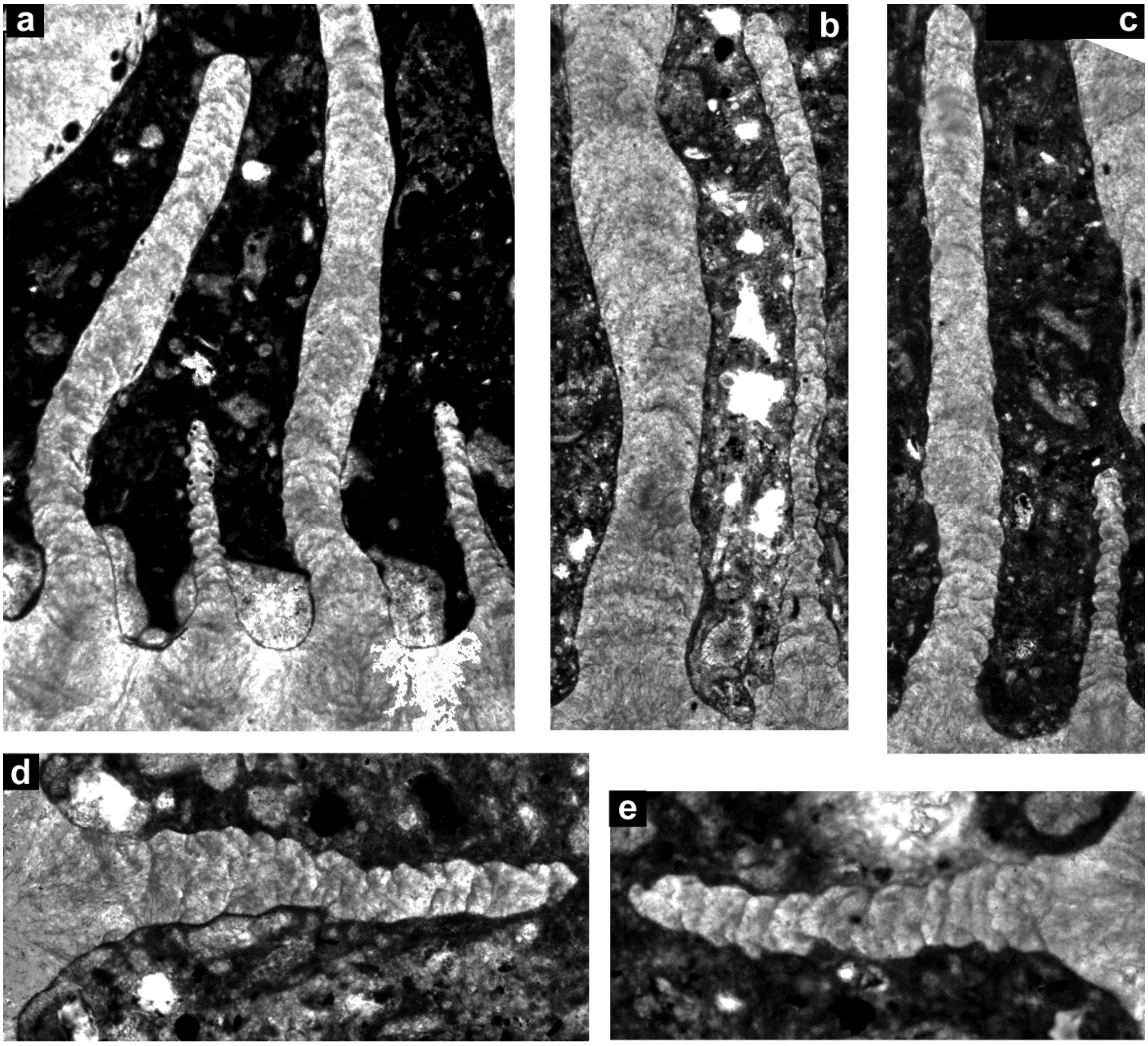


Fig. 4: Fibro-normal septal microstructure of *Ufimia formosa* (SCHINDEWOLF, 1942), holotype; upper Guadalupian (Capitanian, "Basleo-Stage"); Basleo, Timor Island, Indonesia; coll. G. A. F. MOLENGRAAFF, donated to O. H. SCHINDEWOLF (no. X9160, BGR Berlin, figured also in WEYER, 1980a: pl. 4/7–10); cross section no. 4 (middle calice, still without final stereoplasmatic thickening of septal flanks, figured by SCHINDEWOLF, 1942: fig. 62d, pl. 10/1, 11/1). a – first metaseptum and its cataseptum, right cardinal quadrant, x 40; b – left lateral protoseptum and last metaseptum of left antiquadrant, x 40; c – first metaseptum and cataseptum of antilateral septum, left antiquadrant, x 40 (see fig. 7/2a); d – cataseptum in left cardinal quadrant, x 80 (see fig. 7/2b); e – last metaseptum (with still cataseptal habit), left cardinal quadrant, x 80. An unfigured calicular longitudinal section of this holotype (prepared by SCHINDEWOLF) shows one metaseptum cut in more or less median position, with nearly vertical **straight** growth lines (75–80° inclination against the cross section level), there is no indication of former spinose inner septal margins.

Both often rhopaloid protosepta and normal metasepta, and even catasepta, have a special mode of growth in the calice – they do not start as thin filiform dark median line later at the calicular base laterally thickened by stereoplasma, but grow from the beginning at the upper calicular margin in nearly full width with a well-rounded axial end (Figs. 4–7). OEKENTORP (1980, 1984, 2001: figs. 1–3) maintained the diagenetic origin after a then supposed change from aragonitic to calcitic skeleton, which at present is no longer accepted. SORAUF (1983, 1984, in SORAUF & FREIWALD, 2002) strongly favoured the primary biogenic character, also proclaimed by WEYER (1980a).

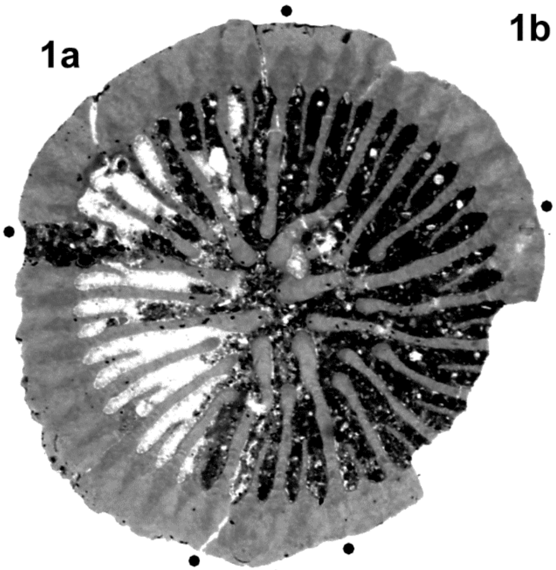
Opposing SCHINDEWOLF's (1942) proof of non-trabicular septa in his studied Plerophyllina, ILJINA (1965, 1984, 1986) everwhere had seen trabiculae in this suborder. We had long discussion on this matter during her Berlin visit in 1976 (cited in ILJINA, 1980: 153), and I proposed her to look at the spinous distal septal margins in the calice as a better argument for the presence of trabiculae: really, she found them in the Upper Emsian *Oligophyllum soshkinae* ILJINA, 1980. But her fanciful drawings of trabiculae in Permian Plerophyllina (1965, 1984) are – sorry to say so – pure imagination, as easily seen in the corresponding photos (e.g. 1965: fig. 10 + pl. 1/2a, fig. 20/1 + pl. 8/1b, c, fig. 31 + pl. 15/6a, b; 1984: fig. 8a + pl. 16/4, fig. 6a, b + pl. 12/5c, 6). She had observed half-moon shaped fans (typical "Septenstirnen"), but reconstructed full-circle trabicular intersections never present in her thin sections.

FEDOROWSKI (1974: 452, fig. 2) also doubted the model of lamellar (= fibro-normal) septal microstructure – without trabiculae – proclaimed by SCHINDEWOLF (1942). His alternative proposal (1974: fig. 2c) was not, though theoretically demanded by him, supported by similar median longitudinal sections within a septum, which SCHINDEWOLF (1942: pls. 1/2–3, 3/3, 6/2) of course had presented with the remark: no sign of any trabiculae. This drawing (1974, fig. 2c) presents the typical "Stirnzonen" = half-moon shaped growth segments (without a continuous narrow dark median line), later (e.g. FEDOROWSKI, 2003a, 2004, FEDOROWSKI & BAMBER, 2001) usually explained as remnants or rudiments of trabiculae, or as recrystallized trabiculae. I cannot follow such incorrect conclusions, even when accepting FEDOROWSKI's "auxiliary" idea of asymmetrical trabiculae (with an elliptical, not circular cross section of the marginal septal spines). The oblique cut of one trabicula in a normal cross section results in an ellipse, where one sector with mostly vertically intersected fibres will not show so clearly the radially arranged calcitic fibres (as shown in fig. 2d, e of FEDOROWSKI, 1974). Such a sector never occurs in "Stirnzonen": they leave no space for a complete circular or elliptical trabicular cut – on the contrary, growth segments are definitively sickle-shaped and follow with a concave base on the broad convex margin of the ancestral one (SCHINDEWOLF, 1942: pls. 7/1b, 11/1, 13/4b; here Figs. 4–7). An additional argument of FEDOROWSKI (2012a: 121) to support his idea, that "Stirnzonen" are not biogenic, seems incomprehensible. There is no logic in postulating that septa like in Figs. 4d, e (without more or less smooth flanks) had their soft body cover reduced to the axial end. One such a septal flank met in a calicular cross section can be compared with the vesicular dissepimentarium surface in a calicular longitudinal section, of course completely covered by soft parts.

Two median longitudinal septal sections in FEDOROWSKI (1974: pl. 63/1, 4) cannot prove the presence of trabiculae = spinous distal septal margins in the genera *Timorphyllum* GERTH, 1921 and *Lophophyllidium* GRABAU, 1928. Already in WEYER (1980a: p. 8) I rejected the trabicular interpretation of these thin sections: "What had been explained by FEDOROWSKI (1974, pl. 63/4) in a median longitudinal septal section between two growth lamellae as trabiculae (alternating light and dark calcite fibres), is also observed in secondary stereoplasmatic thickenings of septa, wall, and tabulae, they are clearly of lamellar microstructure (*sensu* SCHINDEWOLF, 1942: pls. 4/1b, 16/1) governed by a planar control of skeletal secretion. … A comparison with the structure of a Belemnitida rostrum – already done by SCHINDEWOLF (1942) – is useful to understand the septal microstructure of Rugosa. There are alternating light and dark calcitic fibres between two growth lamellae in a belemnitid longitudinal section (MÜLLER-STOLL, 1936: pls. 3/5, 4/1, 5/4 etc.), which in Rugosa could be interpreted as trabiculae; but the belemnitid rostrum has an absolutely smooth [even glossy] external surface."

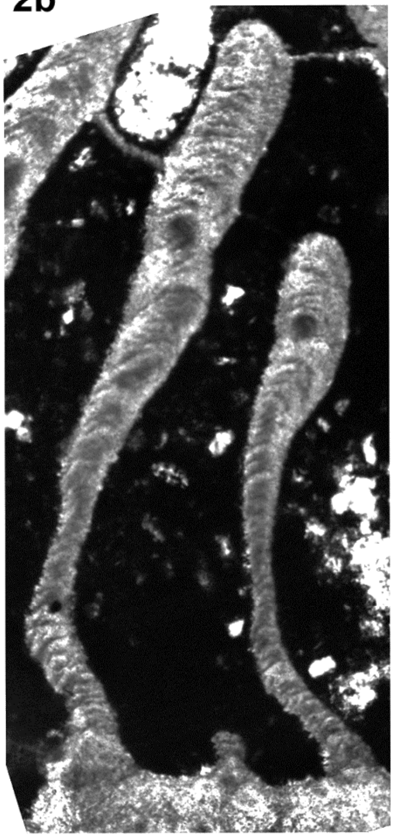
Fig. 5: Fibro-normal septal microstructure of *Ufimia formosa* (SCHINDEWOLF, 1942), upper Guadalupian (Capitanian, "Basleo-Stage"); Basleo, Timor island, Indonesia; coll. EHRAT 1927 (by order of J. WANNER); studied by NIERMANN (1975: 164). Primary septal microstructure with broad half-moon shaped growth segments of major and minor septa. 1 – no. MB.K.7945. (Sé533), locality Basleo-25; (a) cross section no. 4 in middle calice (still without stereoplasmatic thickening layers on the septal flanks), x 8; (b) septal detail (with left antilateral protoseptum in the middle, see fig. 7/3), x 40. 2 – no. MB.K.7946. (Sé552), locality Basleo-7; (a) cross section no. 5 in lower calice (deeper in the cardinal quadrants), x 10; (b) septal detail of cross section no. 6 (middle calice), x 40; (c) cardinal protoseptum of cross section no. 5, x 40 (see fig. 7/4a).

1a

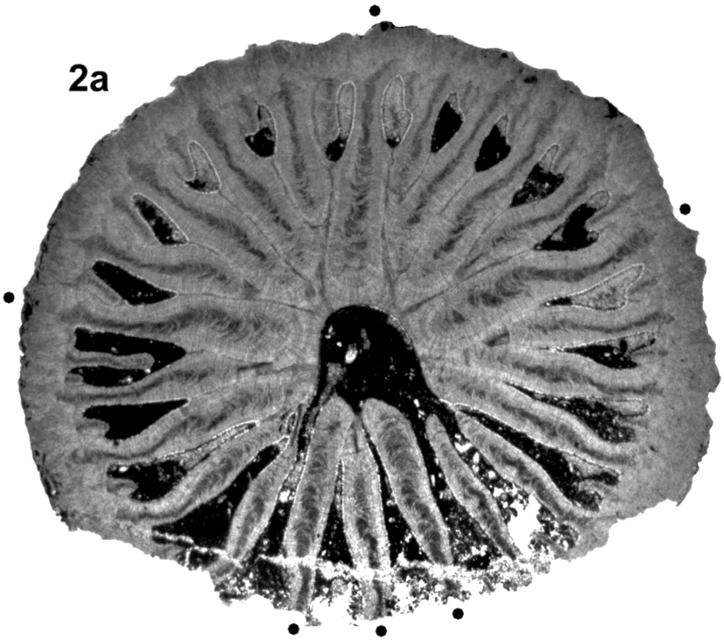


1b

2b



2a



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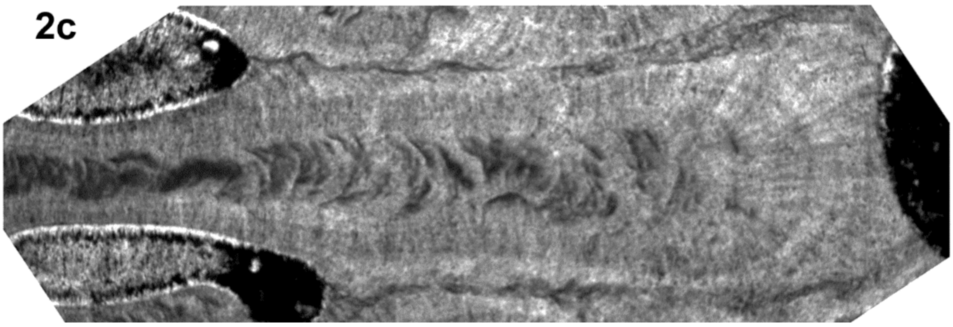

The septal microstructure of several Carboniferous–Permian Plerophyllina and Zaphrentoidina was described by FEDOROWSKI as trabicular. Some more recent examples might be selected: 2003a (pl. 1/4 – *Lophophyllidium* sp.), 2004 (81, pl. 4/3 – *Rotiphyllum exile* DE GROOT, 1963; 86, pl. 5/5,6 – *Ufimia alternans* DE GROOT, 1963), FEDOROWSKI & BAMBER 2001 [47, pl. 7/3a, b – *Allotropiochisma* (*Allotropiochisma*) sp.; 48, pl. 5/5, 7 – *Lytvolasma canadense* FEDOROWSKI & BAMBER, 1001; 51, pl. 7/4, 8/1, 2 – *Ufimia arctica* FEDOROWSKI & BAMBER, 2001; 54, pl. 5/6 – *Calophyllum columnare* (SCHLOTHEIM, 1813); 65, pl. 8/3a, b – *Soshkineophyllum*? sp.; 72. pl. 5/4c – *Tachylasma variabile* (SOSHKINA, 1941)]. All these species possess typical and well-illustrated “Stirnzonen” normally connected with a fibro-normal septal microstructure. In my opinion – with SORAUF (1983, 1984) – it is a primary biogenic, not a diagenetic structure.

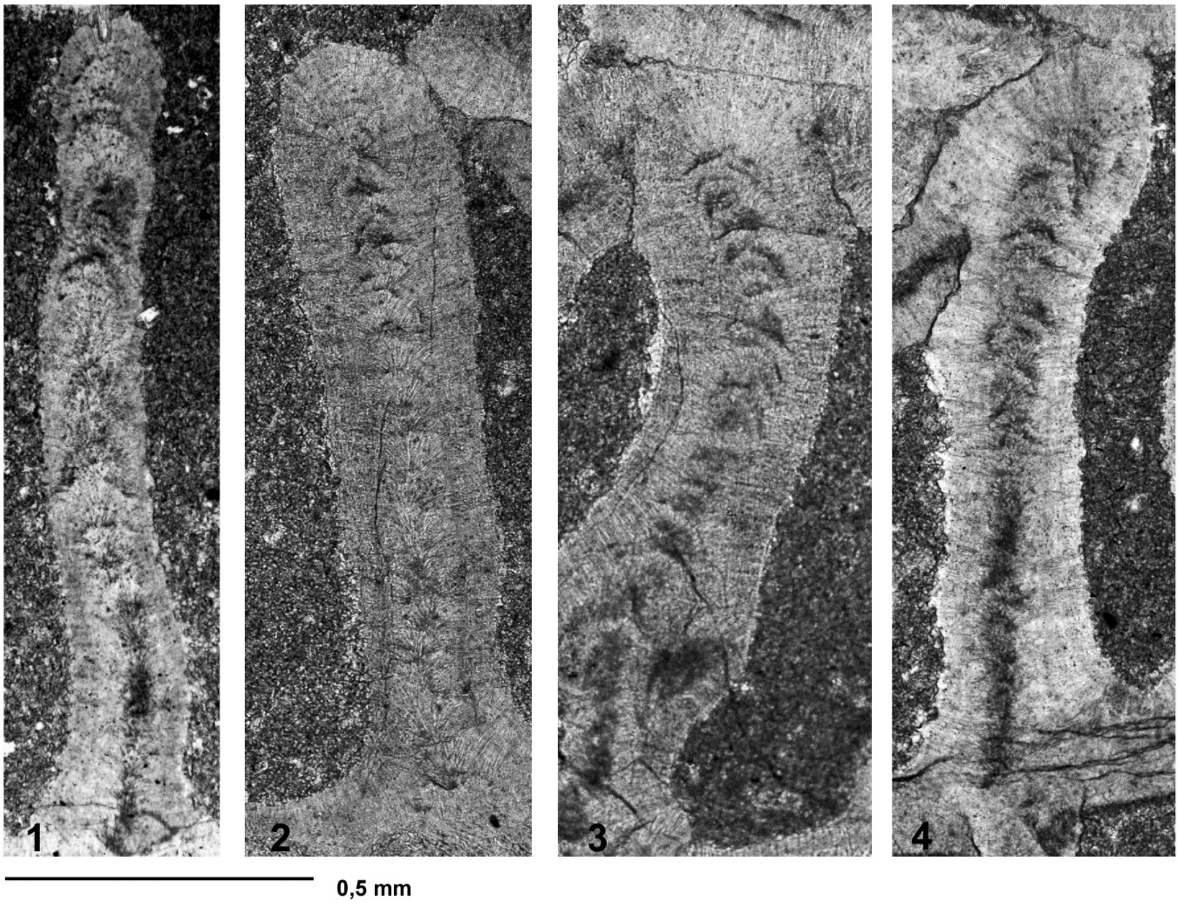

Fig. 6: Fibro-normal microstructure in major septa of *Calophyllum quadrifidum* (HOWSE, 1848), middle Wuchiapingian, basal Zechstein Limestone (Werra Cycle, basinal facies); borehole Friedland 1/1971 (map sheet 1:25000, no. 2247, Spantekow), depth 3795 m, ca. 20 km SSW of Anklam, Mecklenburg-Vorpommern state, NE Germany; coll. R. WALDMANN 1972 (no. X6192, BGR Berlin, figured in WEYER, 1980a: fig. 1/1–3). 1 – thin section no. 8; 2–4, peel no. 14; x 80, mostly well preserved original non-trabicular microstructure with half-moon shaped growth segments and no or weak final lateral stereoplasmatic thickening.

It is really necessary to abandon the old, not yet forgotten opinion that all Rugosa have trabiculae (SORAUF, 1981: 335 – all; ILJINA, 1984: 11 – obviously all; SORAUF & FREIWALD, 2002: 195, 202 – Late Permian *Calophyllum* from Timor island with very small, “invisible” trabiculae). My collections of Wuchiapingian *Calophyllum* from the European Zechstein Basin have smooth distal septal margins. It is recommended to prove the presence or absence of trabiculae by more observations in free and uncorroded calices before starting thin-sectioning.

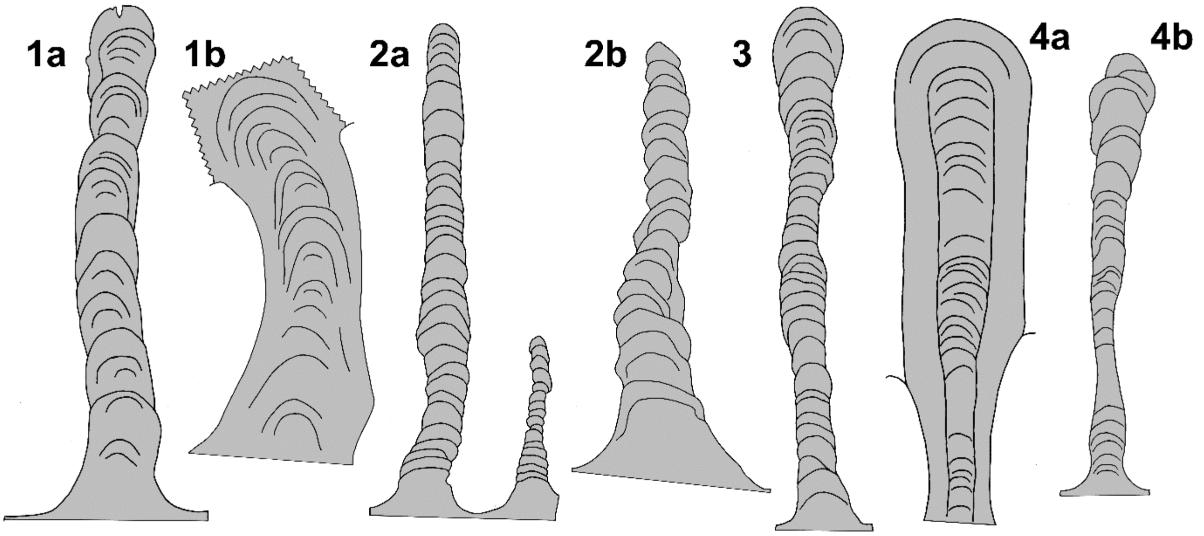

Fig. 7: Selected septa of two Permian Plerophyllina, with fibro-normal microstructure (half-moon shaped growth segments indicating primary skeleton structure, often misinterpreted as secondary = diagenetic and trabicular). Most septa are from middle calicular levels still without final lateral stereoplasmatic thickening, which occurs in the lower calice (1b, 4a). 1 – *Calophyllum quadrifidum* (HOWSE, 1848), specimen of fig. 6, x 50. (a) left lateral septum (see fig. 6/1); (b) right lateral septum (see fig. 6/3). 2–4: *Ufimia formosa* (SCHINDEWOLF, 1942), upper Guadalupian (Capitanian, "Basleo-Stage"), Basleo, Timor island, Indonesia (compare Figs. 4, 5). 2 – no. X9160, BGR Berlin (holotype), coll. G. A. F. MOLENGRAAFF, donated to O. H. SCHINDEWOLF (figured also in WEYER, 1980a: pl.4/7–10); (a) metaseptum and cataseptum, x 25 (see fig. 4c); (b) cataseptum, x 60 (see fig. 4d). 3. no. MB.K.7945. (Sé533), right antilateral protoseptum of fig. 5/1a, 1b, x 25. 4 – no. MB.K.7946. (Sé552); (a) cardinal protoseptum of fig. 5/2a, 2c, x 25; (b) metaseptum of cross section no. 7 (middle calice), x 25.

2.4 The non-trabicular trend

The earliest taxa of all three orders of the superorder Rugosa (Stauriida, Pholidophyllida, Cystiphyllida) in the Ordovician and Early Silurian are characterized by trabiculae representing the plesiomorph phase in phylogeny. As noticed by KATO (1963: 610), this had changed in Carboniferous and Permian times with an increase of taxa having lost their ancestral trabiculae, then replaced by the apomorph fibro-normal septal microstructure or smooth distal septal margins. Such phylogenetical changes where explained by William Dickson LANG (1878–1966) in 1923 for Lower Carboniferous corals (later in 1938 including also Devonian taxa) in his doctrine of trends: Certain morphological features underwent the same changes in quite unrelated evolutionary lines (programme-evolution), often at different times, and appearing within any systematic category (family, genus, species). Here the name **non-trabicular trend** is proposed as a new term useful in Rugosa phylogeny, not as new knowledge – the facts were already well known by KATO (1963). Curiously, SCHINDEWOLF (1942: 28), who discovered the non-trabicular septal microstructure in Rugosa, regarded it as the primitive and ancestral one.

According to our present knowledge, the oldest Rugosa seem to be the Lambelasmatidae WEYER, 1973 (order Stauriida VERRILL, 1865) in the latest Middle Ordovician (top of Darriwilian, upper Llanvirn) of Iran (BAARS et al., 2012). They start in Europe in the Upper Ordovician (Sandbian, Idavere and Johvi stages of Estonia). These first members of the suborder Calostylina PRANTL, 1957 (synonym Monacanthina NEUMAN, 1984) are characterized by coarse and long acanthine trabiculae (monacanths), imperfectly fused forming porous septa (well known in *Coelostylis* LINDSTRÖM, 1880). The transition from trabicular to fibro-normal structure occurred not always sharply. As in the Famennian *Neaxon* KULLMANN, 1965 with septa of both rhabdacanth (uppermost calice) and monacanth structure (main calice, WEYER 1984a: pls. 6/10, 11, 7/15), there might occur comparable septa with a mixture of rhabdacanth and fibro-normal structure (*Rhegmaphyllum* WEDEKIND, 1927 – WEYER 1974: 164) or of monacanth and fibro-normal structure (perhaps still unknown *Oligophyllum* species similar to fig. 8).

Present knowledge has no indication that later members of the Rugosa orders Cystiphyllida NICHOLSON, 1889 and Pholidophyllida WEDEKIND, 1927 ever lost their trabicular microstructure. Ancient Silurian genera of the Cystiphyllida (Cystiphyllidae MILNE-EDWARDS & HAIME, 1850) have acanthine septa; massive blade-like septa built of completely fused trabiculae are attained later in the Middle Devonian (Digonophyllidae WEDEKIND, 1923). Apparently, there exist no cystiphyllid Rugosa with a fibro-normal septal microstructure.

The non-trabicular trend is mainly distributed among the three ahermatypic or cold-water suborders of the Stauriida (according to the classification of HILL, 1981), which I had renamed partially (WEYER, 1991: 11, 1996: 85) applying the principles of priority for the family taxa group (thus anticipating a forthcoming edition of the International Code of Zoological Nomenclature, which does not yet include taxa higher than the family group in its at present available four editions).

The trend is well known in the **Plerophyllina SOKOLOV, 1960** (syn. Polycoeliina KABAKOVICH, 1962, Tachylasmatina FEDOROWSKI, 1973) since the monograph of SCHINDEWOLF (1942). SCHOUPPÉ & STACUL (1959: 238) diagnosed their Zaphrentoidina, which still included the later Plerophyllina, as "Pterocorallia with lamellar septal structure"; but later the presence of trabiculae in some older (Devonian) taxa became slowly evident:

1. KULLMANN (1965: 121) mentioned septal spines in the distal calice of *Oligophyllum* (without estimating the meaning of this feature).
2. SOTO (in SOTO & GARCÍA-ALCALDE, 1976: 97, pl. 1/4–5) and SOTO (1982: fig. 1K–M) illustrated a silicified specimen of *Oligophyllum pentaphylloides* KULLMANN, 1965 (Upper Emsian, Northern Spain) with well-preserved distal septal margins bearing trabicular spines. There was no comment on the taxonomic importance of this feature.
3. ILJINA (1980: 153, 1984: 12, 2/1a, g) proved a trabecular microstructure in *Oligophyllum soshkinae* ILJINA, 1980 (Upper Emsian, Ural Mts) by demonstration of spinous distal septal margins.
4. WEYER (1984b: 20, fig. 4/6, *Pentaphyllum*? n. sp.) presented an unpublished new genus from the uppermost Famennian *Wocklumeria sphaeroides* Zone of the Thuringian Mountains, with well-developed trabecular spines at the distal septal margins.
5. Unpublished new Moroccan Upper Emsian *Oligophyllum* (Figs. 8–10) demonstrate monacanth trabiculae found in upper calicular tangential longitudinal sections. These materials allow the reinterpretation of peculiar crenulated/nodulated septal bases in the cross sections of *Oligophyllum crassum* KULLMANN, 1965 and *Oligophyllum pentaphylloides* KULLMANN, 1965 as trabiculae.
6. The insufficiently prepared cross sections of the Bohemian type material of *Oligophyllum* POČTA, 1902 give no chance to investigate the septal microstructure. But a well-preserved topotype of *Oligophyllum permirum* POČTA, 1902 from the Pragian Dvorce-Prokop-Limestone of Lochkov locality (J. BARRANDE collection, National Museum Praha) has rhabdacanth trabiculae at the uppermost calicular margin.
7. On the other hand, undescribed species with a fibro-normal septal microstructure (well seen as distal calicular smooth septal margins in cast preservation) exist already in the basal Lower Emsian of the German Rhenish Mts. (WEYER, 1973a: 54, fig. 7/5–7). They are now better transferred to *Pentaphyllum*; a second difference (besides the microstructure) against *Oligophyllum* offers the enlarged tabularium.
8. Presumed trabiculae in Carboniferous and Permian Plerophyllina are doubted and should be revised. Their existence mainly proclaimed by ILJINA (1965, 1984), FEDOROWSKI (2004) and FEDOROWSKI & BAMBER (2001) was based on an erroneous interpretation of biogenic "Septenstirnen" as diagenetically altered trabiculae.

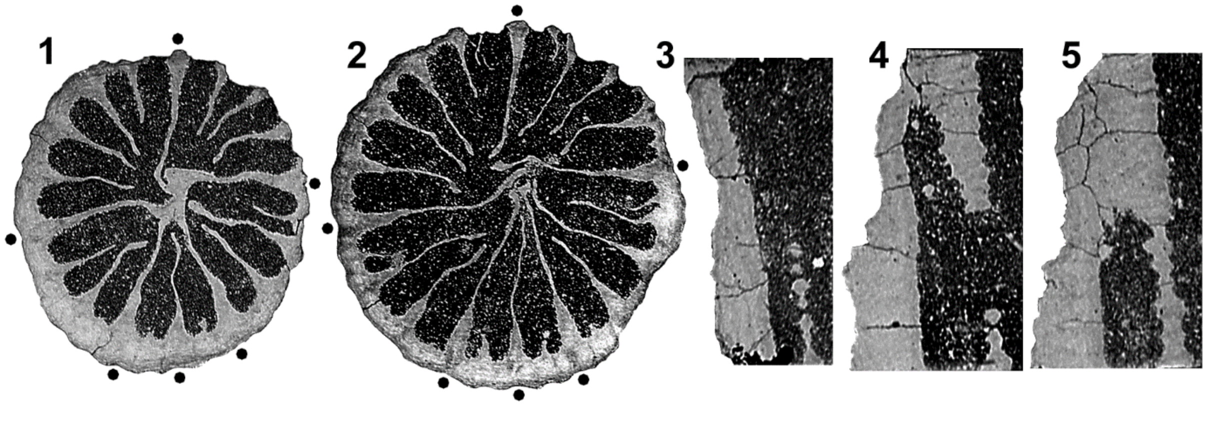

Fig. 8: Trabiculae in the Lower Devonian genus *Oligophyllum* POČTA, 1902. *Oligophyllum* sp. – lower Upper Emsian ("*Gyroceratites gracilis* Zone", *Costapolygnathus laticostatus* Zone, *Nowakia cancellata* Zone), *Hollardops* Limestone Member of the basal Khebchia Formation; locality Bou Tserfine (details of the section: BECKER et al., 2004a: 20, 2004c: 128–132, fig. 2), western Dra valley, southern Anti-Atlas, Morocco; coll. S. SCHRÖDER 2004 (no. MB.K.7940, drawings see fig. 9/1–5). 1, 2 – lower calicular cross sections, x 6 (no.16,14); 3, 4, 5 – tangential longitudinal sections in the uppermost calice, with spinous septal margins, x 10 (no. 3, 4, 6).

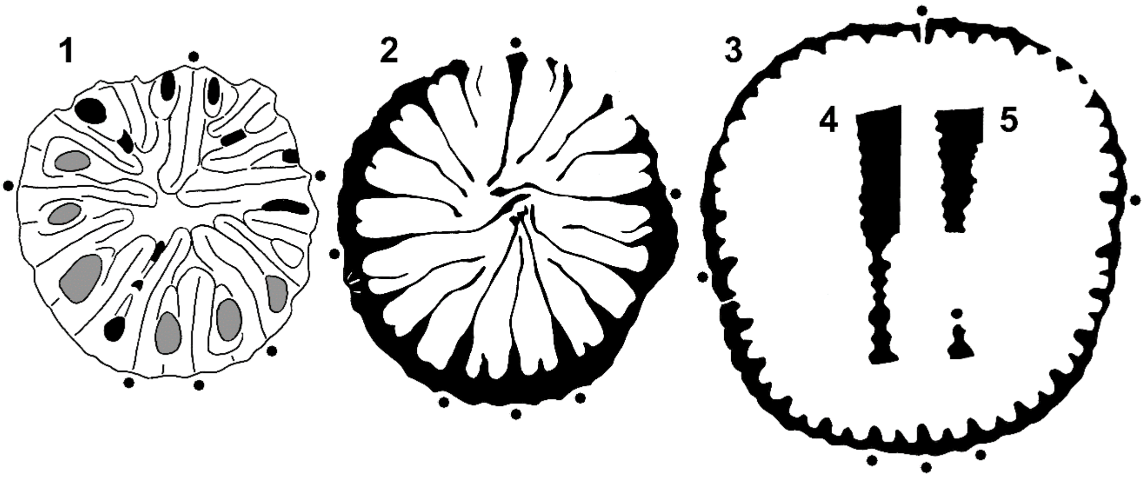

Fig. 9: Trabiculae in the Lower Devonian genus *Oligophyllum* POČTA, 1902. *Oligophyllum* sp. – lower Upper Emsian ("*Gyroceratites gracilis* Zone", *Costapolygnathus laticostatus* Zone, *Nowakia cancellata* Zone), *Hollardops* Limestone Member of the basal Khebchia Formation; locality Bou Tserfine (details of the section: BECKER et al., 2004a: 20, 2004c: 128–132, fig. 2), western Dra valley, southern Anti-Atlas, Morocco; coll. S. SCHRÖDER 2004 (no. MB.K.7940, photos see fig. 8/1–5). 1 – basal calicular cross section, x 10 (no. 16 – skeleton: white; subtabular lumina, filled by sparite: black; calicular lumina with detrital filling: grey); 2 – lower calicular cross section, x 6 (no. 14); 3 – cross section near upper calicular rim, x 3 (no. 7); 4, 5 – two subsequent tangential longitudinal sections in the uppermost calice, with monacanth trabiculae at upper septal margins, x 8 (no. 5,6).

There are at least two unrelated changes in the septal microstructure from trabicular to fibro-normal within the acolumellate members of the suborder **Zaphrentoidina SCHOUPPÉ & STACUL, 1959** (syn. Metriophyllina SPASSKIY, 1965, Stereolasmatina HILL, 1981, Hapsiphyllina NUDDS in NUDDS & LÖSER, 2001). One exists in the family Lindstroemiidae POČTA, 1902, where Devonian trabicular taxa around *Metriophyllum* MILNE-EDWARDS & HAIME, 1850 gave rise to Tournaisian fibro-normal taxa as *Drewerelasma* WEYER, 1973 and *Saleelasma* WEYER, 1970 (WEYER 1994: 195). The difficult proof of smooth distal margins of septa in the calice is indispensable and still missing for e.g. *Drewerelasma omhaense* (LIAO & CAI, 1987) and *Drewerelasma curviseptatum* (LIAO & CAI, 1987) from the basal Tournaisian *Protognathodus kockeli* Zone (*Metriophyllum omhaense* Zone of LIAO & CAI, 1987) in northern Xinjiang. A classification as Lindstroemiidae reflects the phylogenetic relationships already much better than in the second group, the Adradosiinae BIRENHEIDE & SOTO, 1977, put by HILL (1981) and WEYER (1985, though with a completely new diagnosis: "Hapsiphyllidae with a coarse-trabicular septal microstructure) as still a monotypic subfamily into the Hapsiphyllidae GRABAU, 1928, which in general have the fibro-normal structure just as the Zaphrentoididae SCHINDEWOLF, 1938. In HILL (1981), the latter family includes the Cumminsiinae WEYER, 1975, here (fig. 11) used to demonstrate the smooth distal margin of the everted septa.

Obviously, the many pseudocolumellate Zaphrentoidina (Variaxoninae FEDOROWSKI, 2010, Lophophyllidae GRABAU, 1928, Lophophyllidiidae MOORE & JEFFORDS, 1945, Rylstoniidae YÜ, LIN, SHI, HUANG & YÜ, 1983, Wannerophyllidae FEDOROWSKI, 1986, Lophotichiidae WEYER, 1972, Asserculiniinae FEDOROWSKI, 1986, Timorphyllidae SOSHKINA in SOSHKINA, DOBROLYUBOVA & PORFIRIEV, 1941, Verbeekiellidae SCHOUPPÉ & STACUL, 1955) are descendants from different non-columellate genera of the suborder, which all had already attained the fibro-normal stage of septal microstructure. Supposed trabiculae in these taxa should be reinvestigated in view of the smooth distal margins of their septa in the calices.

Trabicular corals represent the majority of the suborder **Cyathaxoniina SPASSKIY, 1977**, but the fibro-normal stage appeared mainly in one line. That is *Cyathaxonia* MICHELIN, 1847 (Cyathaxoniinae MILNE-EDWARDS & HAIME, 1850, Early Famennian–Early Permian) and its immediate ancestor *Laccophyllum* SIMPSON, 1900 (Laccophyllinae GRABAU, 1928). Serious unsolved problems exist within the taxon *Laccophyllum*, covering for the moment both trabicular and fibro-normal species. The latter are e.g. the Famennian *Laccophyllum thuringicum* WEYER, 2004 and Lower Carboniferous species. Trabiculae occur in "*Syringaxon*? sp." of FEDOROWSKI (1997: pl. 2/7, Middle Devonian, Polish Holy Cross Mts.), as seen in free calice with spinous septal margins; I have a similar collection from Moroccan Eifelian–Givetian boundary beds. The septal microstructure of Silurian type species *Laccophyllum acuminatum* SIMPSON, 1900 remains unknown, as in *Laccophyllum lindstroemi* WEYER, 1978 (fibro-normal structure only supposed, not proved). Another family also acquired the fibro-normal microstructure: the Hadrophyllidae NICHOLSON, 1889 with *Angustiphyllum* ALTEVOGT, 1965 (PLUSQUELLEC et al., 2012).

Records of the non-trabicular trend in the other, hermatypic suborders (sensu HILL 1981) are unsure and require intensive investigations. One exception could be *Caninia* MICHELIN in GERVAIS, 1840, but this ahermatypic genus (name giving for the suborder Caniniina WANG, 1950) is mis-classified and unrelated to the majority of conventional so-called "caninioid" taxa. SCHINDEWOLF (1942: 27) cited *Siphonodendron irregulare* (PHILLIPS, 1836) of STRUVE (1898: pl. 5/11) as an example of the fibro-normal septal microstructure in a member of nowadays Lithostrotionina SPASSKIY & KACHANOV, 1971; but SEMENOFF-TIAN-CHANSKY (1984: 489, fig. 1A) found minitrabiculae of 40–60 µm diameter in *Siphonodendron martini* (MILNE-EDWARDS & HAIME, 1851). Previously (SEMENOFF-TIAN-CHANSKY & NUDDS 1979: 251, figs. 1G,2), trabiculae were recorded from *Lithostrotion maccoyanum* MILNE-EDWARDS & HAIME, 1851.

3 The problem of *Pentaphyllum* and Pentaphyllinae

The genus name *Pentaphyllum* DE KONINCK, 1872 is widely used for Devonian–Permian Rugosa, mainly since SCHINDEWOLF (1942). The taxon was based on silicified unicates of two new species found in the Late Tournaisian (Ivorian) of Belgium, using only external and free calicular features before the general introduction of thin section techniques into coral research, and never redescribed from perhaps better preserved topotypes of neighbouring localities (obviously being extremely rare taxa). HINDE (1890: 195) declared *Pentaphyllum armatum* DE KONINCK, 1872 as "the unique typical species" without having seen the specimen – really a bad choice critizised by SCHINDEWOLF (1942: 181), but valid and accepted by FRECH (in ARTHABER 1900: 287), LANG, SMITH & THOMAS (1940: 96) and HILL (1981: F330). Pre-occupation of *Pentaphyllum* DE KONINCK, 1872 by *Pentaphyllus* MEGERLE in DEJEAN, 1821, recent Coleoptera), as suggested by HINDE (1890: 195) and erroneously accepted by CARRUTHERS (1919: 439), HUDSON (1936: 98), and LANG, SMITH & THOMAS (1940: 96), does not exist: the International Code of Zoological Nomenclature declares, that a difference in just one letter prevents homonymy.

It should also be stated that the new genus *Plerophyllum* HINDE, 1890 was not proposed expressly as a replacement name for the presumed homonym *Pentaphyllum* DE KONINCK, 1872 – HINDE (1890: 195) cited *Pentaphyllum* only with question mark as a synonym of *Plerophyllum* and noted some doubts concerning unclear features in the Belgian species. Thus, article 67.8. (International code of Zoological Nomenclature, 4th edition, 1999: homonym and replacement name have the same type species) is not applicable. The designation of *Plerophyllum australe* HINDE, 1890 as the lectotype species of *Plerophyllum* by GRABAU (1928: 46) is valid and was never doubted.

Later authors (e.g. SCHINDEWOLF, 1942: 181) had looked at the *Pentaphyllum* materials stored in the Institut Royale des Sciences Naturelles de Belgique in Bruxelles, but a permission to cut the specimens for thin-sectioning was at first given to FEDOROWSKI (2009a). This revision (also FEDOROWSKI, 2010) concluded (1) that *Pentaphyllum* is a *nomen dubium*, (2) proposed to use instead its synonym *Cryptophyllum* CARRUTHERS, 1919 (based on precisely studied materials), for the moment without any family assignment, thus (3) declaring the subfamily Pentaphyllinae SCHINDEWOLF, 1942 also to become a *nomen dubium*, and (4) replaced the term pentaphylloid mode of septal ontogeny (SCHINDEWOLF, 1942) by "cryptophylloid mode".

Fig. 10: Trabiculae in the Lower Devonian genus *Oligophyllum* POČTA, 1902. *Oligophyllum* sp. – middle Upper Emsian (*Sellanarcestes wenkenbachi* Zone, *Nowakia richteri* Zone, *Linguipolygnathus serotinus* Zone), *Sellanarcestes* Limestone Member of Khebchia Formation; western Dra valley ca. 10 km south of Aouinat Torkoz (N 28°, 23.001', W 9°, 55.076'; locality Torkoz IIa of BECKER et al., 2004a: fig. 2, 2004b: 119, fig. 1, and of JANSEN et al., 2004: fig. 1), southern Anti-Atlas, Morocco; coll. D. WEYER 2007 (no. MB.K.7941.). 1 – external view of corallum, x 1.5 (completely calicular); 2 – lower calicular cross section, x 4 (no. 18); 3 – middle calicular cross section, x 2 (no. 1); 4–8 – tangential longitudinal sections in the lower calice between the two cross sections, demonstrating the monacanth trabiculae at septal margins, x 15 (4 – no. 15, with cardinal septum in the middle, 5 – no. 3) and x 10 (6, 7, 8 – no. 13, 17, 8).

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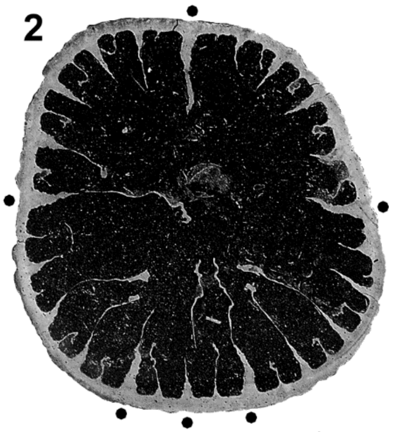

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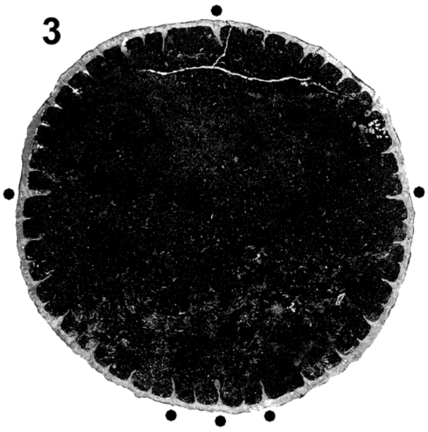

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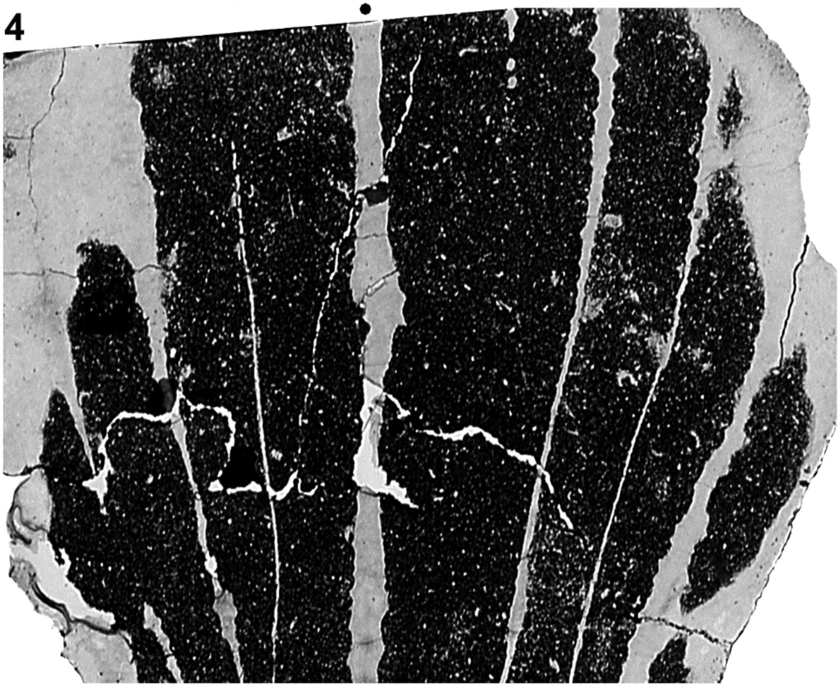

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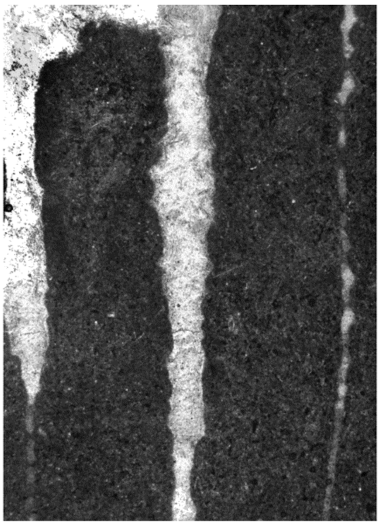

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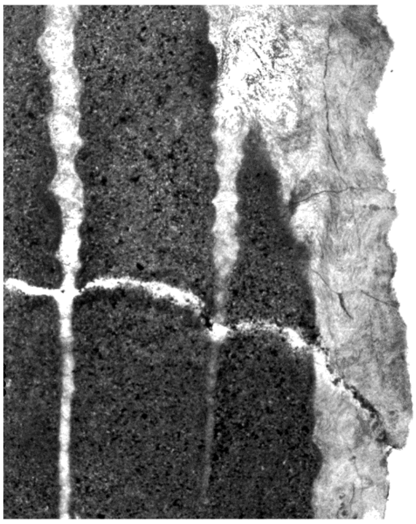

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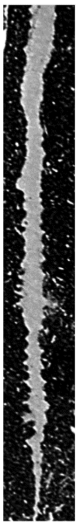

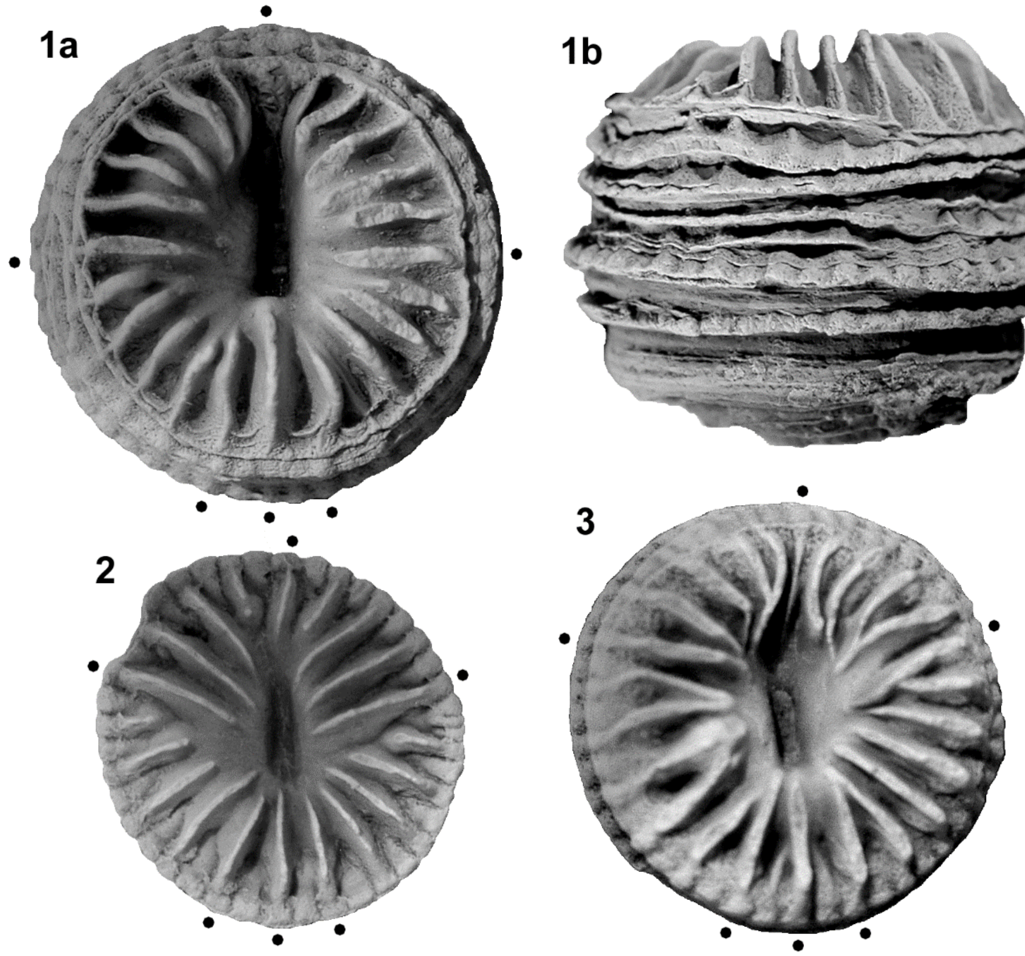

Fig. 11: Smooth distal septal margins (microstructure fibro-normal) of *Cumminsia aplata* (Cummins, 1891), middle Pennsylvanian (lower Moscovian), Smithwick Formation (middle Atokan), Algerita, San Saba county (Texas, USA), coll. D. Korn 2005, x 3. 1a, b. – no. MB.K.7942.; 2 – no. MB.K.7943.; 3 – no. MB.K.7944.

Fedorowski (2009a: 573, repeated in 2012b: 23) also cited the term "tachylasmatoid ontogeny" of Schindewolf (1942: 55 – there "tachylasmoid") as a possible replacement name for pentaphylloid ontogeny but decided not to employ it for the time being because of all the uncertainties up to now connected with the genus *Tachylasma* Grabau, 1922 and its unknown ontogeny. This is an error: the term "tachylasmoid" (recte tachylasmatoid) ontogeny was used by Schindewolf in the sense of Hudson (1936: 92, fig. 1 – tachylasmoid trend *sensu* Lang, 1923) meaning the non-pinnate, sometimes Scleractinia-like "cyclic" alternating of longer, often rhopaloid protosepta and metasepta in the adult phase. A further error in Fedorowski (2009a: 571, 578) is the statement, that Schindewolf (1942) had declared *Pentaphyllum armatum* de Koninck, 1872 and *Pentaphyllum caryophyllatum* de Koninck, 1872 to be synonyms; he always had kept them separately and congeneric in 1942.

This dilemma around *Pentaphyllum* is every day's job in palaeontology. In 1872, the two specimens now called holotypes really were new taxa, studied with the methods of the time, and justifying the introduction of a new genus. Meanwhile, new techniques (thin sectioning, x-ray studies, and scanning electron microscope) wait for much better preserved and richer populations, and the original "collection" is insufficient. The main deficit is the extremely small, even decreasing number of specialists collecting and studying such small and rare ahermatypic Rugosa.

One solution to retain and redefine the present nomen dubium *Pentaphyllum* could be to apply to the International Commission on Zoological Nomenclature to allow a change of its type species: as in the comparable, though much more important case of *Archaeopteryx* Meyer, 1861, which was originally based on an isolated undeterminable "bird" feather. *Pentaphyllum caryophyllatum* de Koninck, 1872 had always been estimated as the better genotype, and of course Fedorowski (2009a) included it into the junior synonym *Cryptophyllum*. Perhaps, the species was also found in England by Hudson (1936: pl. 5/2a–d, including one paralectotype of *Cryptophyllum hibernicum* Carruthers, 1919, both determined as *Cryptophyllum* *caryophyllatum* (in this followed by SCHINDEWOLF, 1942: 173, fig. 73, but opposed by FEDOROWSKI 2009a: 581 thinking about a separate new Irish species). These taxa are part of a rather diversified, not yet finally elaborated species group in the Upper Tournaisian of Western and Middle Europe, including also *Pentaphyllum hithis* WEYER, 1975 from extremely rich communities found in boreholes on the island of Rügen (WEYER, 1975a, 1993). Such faunas with many still unknown species need intensive restudies before getting a better taxonomical understanding – this will be the only chance after all to find for the first time a second European specimen with the peculiar morphology of the *Pentaphyllum armatum* holotype, with our actual knowledge nearest to the monotypic *Pseudocryptophyllum* EASTON, 1944 (Chouteau = Middle–Upper Tournaisian of Missouri). Silurian specimens assigned with some reservation ("cf.") to *Pseudocryptophyllum* (SUTHERLAND, 1965: 42, Ludlow of Oklahoma) – remarkable homoeomorphs of the Permian *Hexalasma primitivum* SOSHKINA, 1928 – still are stratigraphically isolated.

The present type species *Pentaphyllum armatum* DE KONINCK, 1872 differs from the generally accepted diagnosis of *Pentaphyllum* or *Cryptophyllum* by its six prominent protosepta, for the first time correctly illustrated in FEDOROWSKI (2009a: fig. 2B, E – antiseptum long, not shortened). This seems to remind the Early Permian "Hexalasmatidae SOKOLOV, 1960" and to exclude any affinities with "Pentaphyllidae". The taxonomical value of this longer or shorter antiseptum is the unsolved problem. At first, the photographs in FEDOROWSKI (2009a: fig. 2B, E) clearly demonstrate that the two neighbouring antilateral septa meet axially and include the antiseptum, which therefore is a little bit shorter (as a first tendency, at least in the mature calice; the ontogenetical behaviour remains unknown).

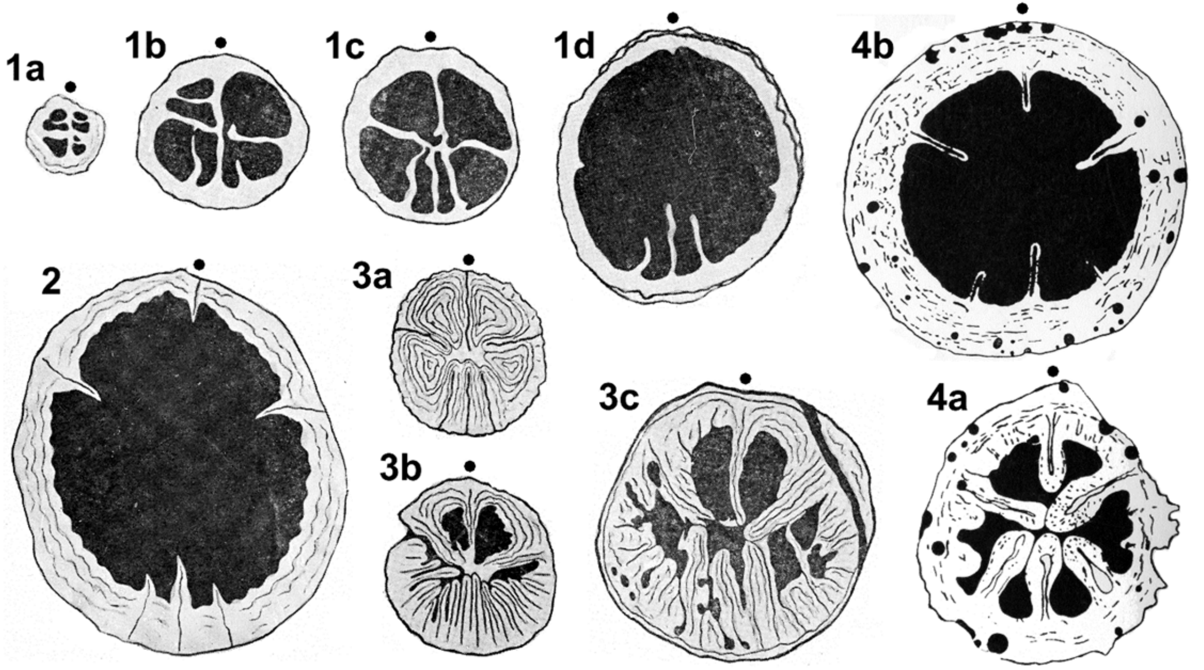

Fig. 12: Species of *Hexalasma* SOSHKINA, 1928, and their antiseptum. 1a–d – *Hexalasma primitivum* SOSHKINA, 1928, holotype (PIN Moskva, no. 146/498), serial cross sections, x 4; Orlovka Formation, Sargian Substage, Upper Artinskian; river Shchugor (middle steep riverside), western slope of northern Ural; coll. E. D. SOSHKINA ca. 1925 (copied from SOSHKINA, 1928: fig. 11a–d, with corrected orientation of the septal apparatus in 1a, 1b, and 1d). 2 – *Hexalasma hexaseptatum* (SOSHKINA, 1928), paralectotype (PIN Moskva, no. 146/419, designated by SOSHKINA et al., 1941: 49, 287), calicular cross section, x 2.5; Orlovka Formation, Sargian Substage, Upper Artinskian; river Shchugor (4 km upstream its mouth), western slope of northern Ural; coll. T. A. DOBROLYUBOVA ca. 1925 (copied from SOSHKINA ,1928: fig. 7e). 3a–c – *Hexalasma hexaseptatum* (SOSHKINA, 1928), lectotype (PIN Moskva, no. 146/418, designated by SOSHKINA et al., 1941: 49, 287), serial cross section, x 2.5 (a, b) and x 3 (c); Orlovka Formation, Sargian Substage, Upper Artinskian; river Shchugor (4 km upstream its mouth), western slope of northern Ural; coll. T. A. DOBROLYUBOVA ca. 1925 (copied from SOSHKINA, 1928: fig. 7b–d, with corrected orientation of the septal apparatus in 3a). 4a–b – *Hexalasma*? *protoseptatum* SOKOLOV, 1960, holotype (institutional/museal deposit unknown, perhaps an interpretation of the unique specimen as a member not of Plerophyllidae/Pentaphyllidae, but of Polycoeliidae is more probable), serial cross sections, x 2; Khivach Formation, Dzulfian/Wuchiapingian; Khivach river, upper Gizhiga river basin, southeastern Omolon Mountains, East-Sibiria; coll. V. M. ZAVODOVSKIY 1941–1946 (copied from SOKOLOV, 1960: pl. 1/1–2).

The here described new genus *Thurispina* offers an unexpected high intraspecific variability in this feature. Sometimes, the antiseptum is long from the beginning and at maturity very slightly shortened (holotype, fig. 15), or always long (fig. 16), or in middle phases shortened and adult as long as the antilateral septa or very slightly shortened (fig. 19, 18/1–12), or in middle and adult phases shortened with one calicular long appearance (fig. 17). A comparable variation occurs in the Cisuralian (late Artinskian) *Hexalasma* SOSHKINA, 1928 (figs. 12, 13). The revision of ILJINA (1984: 88) declared the genus to be a synonym of *Pentaphyllum* DE KONINCK, 1872 (similar as SOSHKINA, et al. 1941: 51 – synonym of *Tachylasma* GRABAU, 1922), and rejects a family Hexalasmatidae Sokolov, 1960. The type species *Hexalasma primitivum* SOSHKINA, 1928 was understood as the juvenile stage of *Tachylasma hexaseptatum* SOSHKINA, 1928. The surprising variation in the length of the antiseptum (in comparison with the two antilateral septa) is remarkable, especially its juvenile length, which has caused an occasional classification of *Hexalasma* as Polycoeliidae DE FROMENTEL, 1861 (SCHINDEWOLF, 1942: 91, 176; HILL, 1981: F324). For the moment, we have to accept the enormous variation, until a future intensive study of populations from the two neighbouring localities at the river Shchugor might prove or disprove this opinion. Of course, an alternative conception as two species of two different genera seems also possible.

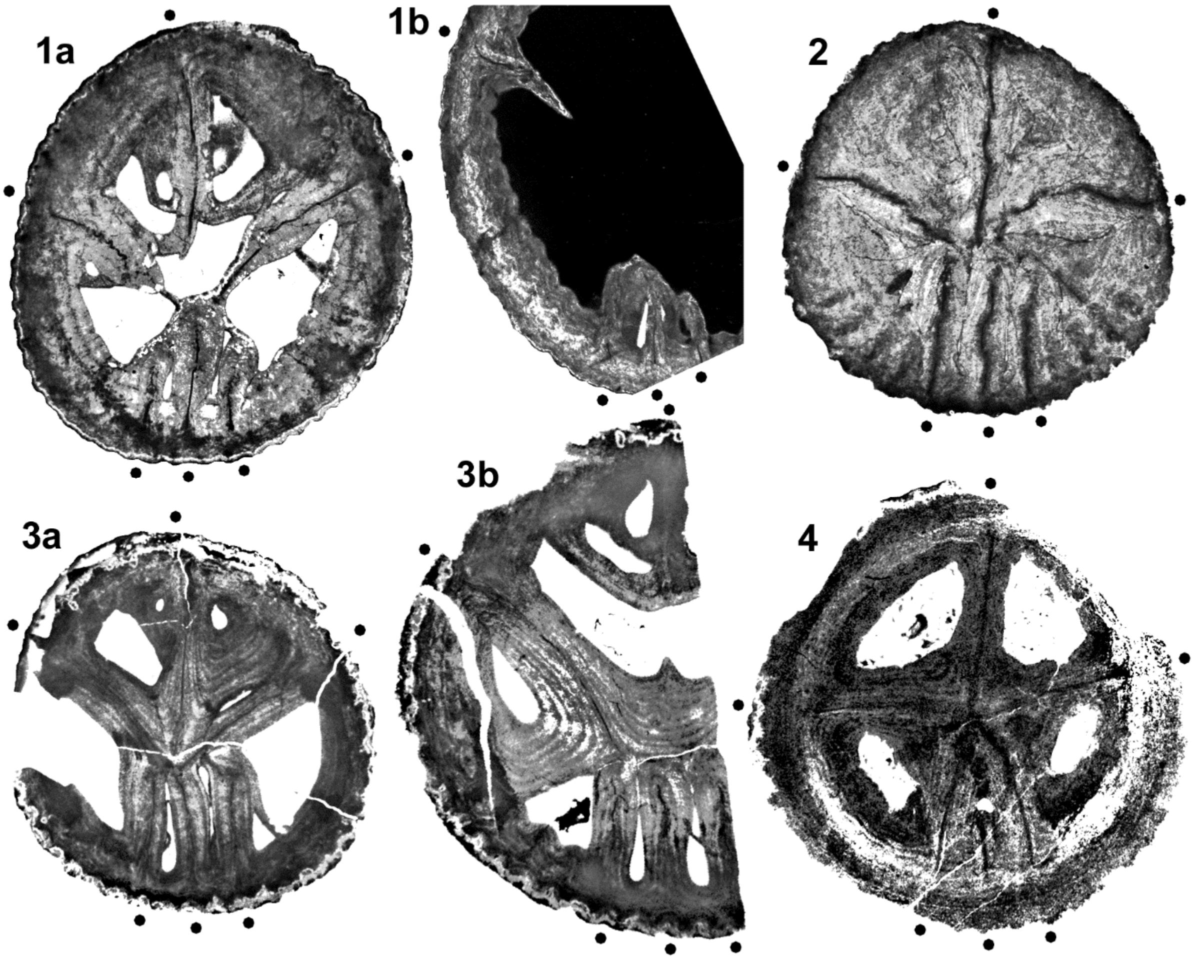

Fig. 13: Antiseptum in paralectotypes (PIN Moskva) of *Hexalasma hexaseptatum* (SOSHKINA, 1928); Orlovka Formation, Sargian Substage, Upper Artinskian; river Shchugor (4 km upstream its mouth), western slope of northern Ural; coll. T. A. DOBROLYUBOVA ca. 1925 (fotos O. L. KOSSOVAYA, VSEGEI St.–Peterburg). 1a–b – subtabular and calicular cross section, x 3 (no. 146/425, figured ILJINA, 1984: pl. 6/4, 7/2a–c). 2 – subtabular cross section, x 4 (no. 146/427, figured ILJINA, 1984: pl. 7/3a–b). 3a–b – subtabular cross section, x 4 (no. 146/1051, figured ILJINA, 1984: pl. 6/3a–b, 7/1a–b, and KOSSOVAYA, 2007: pl. 2/1–5). 4 – subtabular cross section, x 5 (no. 146/1054, figured ILJINA, 1984: pl. 7/4).

Such reasons stimulate me not to abandon *Pentaphyllum* in favour of *Cryptophyllum* (and *Tachylasma* in favour of *Effigies*), and to underline the urgent necessity of modern morphological-taxonomical revisions before forgetting the ancient taxa.

A case similar to the situation of *Pentaphyllum* DE KONINCK, 1872 is the genus *Tachylasma* GRABAU, 1922, base for a family Tachylasmatidae GRABAU, 1928 and a suborder Tachylasmatina FEDOROWSKI, 1973, in principle with the present state of knowledge also a *nomen dubium*. This was the procedure of FEDOROWSKI (2012b: 23, 24), when he proposed *Effigies* gen. nov. with the type *Pentaphyllum* (*Tachylasma*) *silesiacum* SCHINDEWOLF, 1952 (Late Serpukhovian), provisionally placed into an suborder *incertae sedis*. SCHINDEWOLF (1942) used the taxon conditionally because of the unknown ontogeny of its type species *Tachylasma cha* GRABAU, 1922. This taxon was never revised seriously in Chinese literature. There are some, mostly isolated and adult illustrations of cross sections identified as *Tachylasma cha* which say nothing about the early, either zaphrentoidid or pentaphylloid ontogeny (ZHAO, 1976: 218, pl. 1/9a–c; FAN, 1978: 151, pl. 50/4, 7; JIANG, 1982: 86, pl. 62/6; ZHU et al., 1982: 114, pl. 32/3). Only CHI (1937: 86, pl. 2/1a–d) published a series of four cross sections, which might indicate – not for sure, as the smallest section has already a diameter of 7 mm – rather a zaphrentoidid than a pentaphylloid ontogeny, but there is no certainty that his specimens from the Chihsia-Limestone (Late Cisuralian) of western Kiangsi province are really conspecific with the *cha*-holotype coming from a somewhat uncertain locality. SCHINDEWOLF (1942: 190) was fully aware of the problematical taxonomy of *Tachylasma* in GRABAU (1922, 1928) without future ontogenetic research and guessed that some of his species belong to *Ufimia* STUCKENBERG, 1895 (with zaphrentoidid mode of ontogeny). This I can confirm for *Ufimia lopingensis* (GRABAU, 1928) after studying the Rugosa of the Wuchiapingian RICHTHOFEN collection from Loping, determined by KAYSER (1883: 194, pl. 29/7–10 pars) as *Lophophyllum proliferum* (MCCHESNEY, 1860), and already revised by HUANG JI-QING (1904–1995) – according to a label in his handwriting – as *Tachylasma lopingense* during a Berlin visit before the publication of his 1932 monograph.

4 Primary calice-ontogeny and secondary postcalice-ontogeny

Traditionally, the ontogeny of solitary Rugosa is studied by means of a series of cross sections with special attention to the juvenile tip. This method is partly correct, but includes also a fundamental error: principally subtabular sections offer only the skeleton configuration achieved at the base of the calice, but cannot answer all questions, how this morphology was constructed. Therefore, a proposal (WEYER, 2005) demands two series of cross sections to analyse a primary or calix-ontogeny and a secondary or postcalix-ontogeny. The first way examines the complete calice from top to base – against the general growth direction; the second is the classical study of subtabular regions from the larval tip to the calicular base.

A calice-ontogeny starts with the statement that growth (with many diverse vectors) of any cross section level begins at the uppermost calicular rim and ends at the calicular base, where the soft parts then will “leave” (atrophy, tractive updrawal, hydraulic up-pushing) their former skeleton by secretion of new basal elements (tabulae, tabellae, dissepiments, stereoplasma). Many narrow-positioned cross sections elucidate how the skeleton changed slowly from its top-calice-picture towards its base-calice-picture. This increase may be very complicated in cases of different axial structures, pali, carinae, or extremely deep calices. In principle, such an analysis studies the complete calicular morphology of only one life phase, but allows to understand the ontogenetic skeletal growth in one cross section level with all its different horizontal, oblique, vertical, centripetal, centrifugal, and tangential vectors. Deplorably, the method is used seldom due to the fatal old recommendation to study a solitary Rugosa by one cross section near or just below the calicular base and by one longitudinal section there-under (suitable only in the 19th century, when preparing thin sections was still rare). Thus, we had to live with a long period nearly neglecting calicular features. Of course, this analysis against the summarized vertical growth contradicts the increase in septal number, but reflects the synchronous events of skeleton secretion in a deep three-dimensional calice. Today, modern x-ray techniques will provide even better results, if the calicular sediment filling offers the necessary contrast.

The necessity of special calice-ontogenetic studies was connected with the unfortunate subdivision of the genus *Polycoelia* KING, 1849 (junior synonym of *Calophyllum* DANA, 1846) by SCHINDEWOLF (1942: 66): subgenera *Tetralasma* SCHINDEWOLF, 1942 and *Weissermelia* SCHINDEWOLF, 1942 (homonym of *Weissermelia* LANG, SMITH & THOMAS, 1940, replaced at first by *Pleophyllum* LECOMPTE, 1952, and later also by *Pycnocoelia* SCHINDEWOLF, 1952). Diagnoses proposed by SCHINDEWOLF for these three subgenera strongly violated the principle of homology – he had compared (in part based on poorly preserved unicates) initial middle calicular, more advanced basal calicular, and final subtabular structures, which can be found in one specimen. Here this primary calice-ontogeny thinking is necessary to understand the pentaphylloid mode of septal development in several Plerophyllina.

5 Plerophyllina with trabicular septal microstructure

The increasing, but still imperfect evidence for the existence of trabicular septal microstructures in Devonian and Silurian Plerophyllina demands a reclassification, which necessarily can be only rather temporary, not yet cladistic. Concerned genera are near to the families Plerophyllidae KOKER, 1924 and Pentaphyllidae SCHINDEWOLF, 1942. Probably trabiculae occur also in ancient Polycoeliidae DE FROMENTEL, 1861 – perhaps the Lochkovian *Amandaraia* LAVRUSEVICH, 1968, the Emsian *Tetraphyllia* YOH, JIN, ZHEN & XIE, 1984, the Eifelian *Gerolasma* GLINSKI, 1999, and the Ludlowian "cf. *Pseudocryptophyllum* sp. A" of SUTHERLAND (1965) might be candidates. There is also a stratigraphically unexpected, undescribed Pragian *Calophyllum*? n. sp. from Bohemia (with unknown microstructure), occurring together with the classical *Oligophyllum* POČTA, 1902.

YOH et al. (1984: 5, pl. 1/1–6) and again JIN (2005: 138, pl. 24/6–16) described their new genus *Tetraphyllia* as a member of the superorder Heterocorallia SCHINDEWOLF, 1941. This is incorrect, as the wall is not a heterotheca (growing from inside outward), but an archaeotheca with opposite growth direction, typical for most Rugosa (WEYER, 1995: 112). A subfamily Tetraphylliinae YOH, JIN, ZHEN & XIE, 1984 might be available, if these Upper Silurian, Lower Devonian, and Eifelian Polycoeliidae should have trabiculae. Moreover, perhaps *Tetraphyllia* might support the suspicion of SCHINDEWOLF (1942: 64, fig. 22, *Polycoelia*? sp., Lower Brigantian, Upper Viséan) about the existence of a "tetraphylloid" ontogenetic mode of some Polycoeliinae, analogous to the pentaphylloid mode of his Pentaphyllinae.

The actually best solution seems to be a non-phylogenetical "horizontal" taxonomy using the already existing subfamily Anisophyllinae IVANOVSKIY, 1965 with a completely changed diagnosis (Pentaphyllidae with trabicular septal microstructure) to include the following genera:

1. *Oligophyllum* POČTA, 1902 – up to now, this most widespread, mainly Early Devonian genus differed from *Pentaphyllum* by its extremely deep calice and the nearly absence of tabulae. Here its trabiculae, unfortunately still unknown in the type species *Oligophyllum quinqueseptatum* POČTA, 1902 (only fragmentary holotype available), first found in Spanish and Russian materials, are presented from a Moroccan collection (Figs. 8–10). *Pentelasma* KULLMANN, 1965 is included as a synonym.
2. *Pentaxon* GLINSKI, 1999 – at present known only by the holotype of the type species *Pentaxon struvei* GLINSKI, 1999 (Givetian Loogh-Formation, Eifel region of Rhenish Mts.). Trabiculae are well seen in the longitudinal section (1999: 111, pl. 2/10) as spines at former distal margins of a septum. The genus differs from the other members of the subfamily by its special aulos-like, not everted axial structure.
3. *Thurispina* nov. gen.
4. *Anisophyllum* MILNE-EDWARDS & HAIME, 1850 – The type species *Anisophyllum agassizi* MILNE-EDWARDS & HAIME, 1850 (Ludlow, Brownsport Formation, Tennessee) was well revised by ILJINA (1978). Her first thin sections (pl. 5/7; 1984: pl. 4/1v, g) show trabiculae, reconstructed in her drawings (fig. 3) sowewhat exaggerated. They should be visible also in the available free calices (pl. 5/3a), but there the septal margins mostly are smooth (supposed to be destroyed?), as also in AMSDEN (1949: pl. 25/18, 19). This must be tested once more in well-preserved collections offering the primary structure in spite of silicification. Perhaps the marginal spines are restricted to the uppermost calicular regions and disappear deaper (especially on the three prominent rhopaloid septa), as in the excellent specimen of SUTHERLAND (1965: pl. 34/5), which was determined *Anisophyllum*? sp. Contratingent catasepta (described by AMSDEN, 1949: 104, and illustrated by ILJINA, 1978: 33, fig. 1k, pl. 5/1v) are a rather apomorph feature for this Ludlow age.

The early ontogeny of some of these corals offers interesting aspects. The antiseptum is present from the beginning and with a prominent length in *Oligophyllum soshkinae* ILJINA, 1980 (1984: fig. 28) and in *Thurispina jogi* nov. sp. (fig. 15). Thus they are comparable to the few observations made in the Uppermost Early Carboniferous (Late Serpukhovian) and in the Middle/Late Permian: *Tachylasma silesiacum* (SCHINDEWOLF, 1952) (WEYER 2008: fig. 1/3, 4), *Pentaphyllum breviseptum* (ILJINA, 1962) (ILJINA 1984: fig. 9), *Pentaphyllum dzhulfense* (ILJINA, 1962) (ILJINA, 1965: fig. 17), *Pentamplexus minimus* (ILJINA, 1965) (ILJINA, 1984: fig. 45), *Tachylasma gracile* (SCHINDEWOLF, 1940) (SCHINDEWOLF, 1942: fig. 85; WEYER, 1980a: pl. 4/1–6, ILJINA, 1984: fig. 42, pl. 14/2). The antiseptum is best visible in species with a well developped archaeothecal longitudinal ribbing. It appears after the secretion of the aseptal prototheca (*sensu* BERNARD, 1904), and it disappears within the thickening wall during the first phases of the primary or calyx-ontogeny – that means the antiseptum was already and always active at the uppermost calicular margin and becomes reduced later only in deeper parts of the calice (there not longer being for a certain period of the early life a protuberance into the coral lumen). Thus the distinction between a reduced or underdeveloped antiseptum (FEDOROWSKI, 2009a: 5474) is not accepted – with the first appearance of the external septal groove (after the prototheca), the antiseptum persists continuously in the upper calice. An additional distinction between foundation or bases of septum and septum is unnecessary: both are the same septal structure, starting at the upper calicular rim similar to my picture reproduced in HILL (1981: F12, fig. 5/1). This affords to see the growth of a standard solitary Rugosa with its primary or calyx-ontogeny and with its secondary or postcalyx-ontogeny (presenting only a series of basal calicular stages).

The case is more difficult in those many corals without external longitudinal ribs and septal furrows. Relevant cross sections of the uppermost calice are rare, but demonstrate nearly the same septal configuration as Rugosa with septal furrows: *Bathybalva crassa* WEYER, 1981 (pl. 4/19), *Neaxon regulus* (RICHTER, 1848) and *Neaxon cheilos* WEYER, 1984 (pl. 6/10, 7/15), *Pentaphyllum walliseri* WEYER, 1994 (fig. 10/5, 13), *Guerichiphyllum*? *mirabile* WEYER, 2002 (fig. 1/12). A reduction of such septa, if present, within the stereplasmatic thickening of the archaeotheca often is no longer visible in diagenetically recrystallized material. A remark of FEDOROWSKI (2009a: 575) "Bases of septa and short septal blades are always present in the upper parts of mature calices when septal grooves were developed, and never when they did not" is at least disputable. ILJINA (1984: fig. 33a, pl. 5/1a, 1b) proposed a drawing (paralleled by a photo) of the earliest septate cross section of the lectotype of *Cryptophyllum hibernicum* CARRUTHERS, 1919 – the material, on which the pentaphylloid mode of early protoseptal genesis was based – with the antiseptum seen inside the wall. I would not deny this picture, though of course a better diagenetically unchanged calcite preservation might be wanted. SCHINDEWOLF's best example for his pentaphylloid mode among the own materials was the Mid-Permian *Tachylasma gracile* (SCHINDEWOLF, 1940) in the usually good preservation of Timor collections, figured in 1942 (fig. 85a–c = pl. 32/1a–c) – here the reduced septa (including the antiseptum) are also visible inside the wall (WEYER, 1980a: pl. 4/1–3,5; ILJINA, 1984: fig. 42a–c = pl. 14/2a–c).

Recently the difficult boundary between the zaphrentoid and pentaphylloid (or now cryptophylloid) mode of septal ontogeny was redefined (FEDOROWSKI, 2009a: 573, fig. 1). He chose the zaphrentoid first septum, the axial septum (connected cardinal and antiseptum) as the decisive criterion, said not developed in the pentaphylloid mode. Thus some traditional examples of the pentaphylloid mode were reinterpreted as variants of the common zaphrentoid mode: *Oligophyllum soshkinae* ILJINA, 1980 pars, *Pentaphyllum breviseptum* (ILJINA, 1962), *Pentaphyllum dzhulfense* (ILJINA, 1962), *Pentamplexus minimus* (ILJINA, 1965), figured in ILJINA (1965: fig. 17; 1984: fig. 9, 28, 45); this would include also the here described *Thurispina jogi* nov. sp. I am not convinced that the antiseptum really is missing at the beginning of the pentaphylloid mode of septal ontogeny, and I always would try to find it within the thickened archaeotheca. This was the reason, why ILJINA (1965) and WEYER (1972) did see no sharp distinction, but gradual transition between the two modes.

The presence of external septal furrows on the archaeotheca was estimated by FEDOROWSKI (1991: 417) as a perhaps apomorphic feature, preceded in phylogeny by a smooth wall bearing only growth lines (as plausibly underlined by the prototheca). However, the trend had been running in the opposite direction. The great majority of Ordovician Stauriida (Calostylina, Streptelasmatina) constructed an externally ribbed wall after the first postlarval, still aseptal skeleton of the prototheca. This first phase still without any septa is well described by BROWN (1909: 52, figs. 1–6) for "*Lambeophyllum profundum*" (CONRAD, 1843), the oldest North American Rugosa species from the Blackriverian (Upper Ordovician, Late Sandbian) – his illustrations are not drawings of thin sections, but "sectional views" of complete juvenile specimens, etched out from limestone by acid and looking into their calices; the prototheca is a smooth hollow cone of 2 mm length and 1 mm in diameter.

6 *Thurispina* nov. gen.

The new coral taxon occurs in the last Upper Famennian ammonoid zone of *Wocklumeria sphaeroides* (RICHTER, 1848) in the Saalfeld area (near the classical Bohlen outcrop) at the southeastern flank of the Schwarzburg Anticline (fig. 14). A precise map with the type locality Fischersdorf-East and its section are published in BARTZSCH & WEYER (2012: 11, figs. 4, 6b). The horizon is in the uppermost layers (beds 32.6–10.) of the Breternitz Member (former Upper Clymeniid Beds), Gleitsch Formation, Saalfeld Group, immediately below the global Hangenberg-Event (bed 32.12.). It is a basinal facies of shales (with entomozoid ostracods) and limestone nodules. The fauna was only available in 1954 during an intensive collecting period for mainly ammonoids. The second locality Zopten (SW of Probstzella – Fig. 14) is situated at the Gräfenthal Horst, northwestern flank of the Ziegenrück Syncline, in the same horizon; the specimen was collected by chance at the end of the 19th century, perhaps in the mapping period of the Royal Prussian Geological Survey. Unfortunately, the new species was not found again during the extensive fossil collectiona of BARTZSCH & WEYER (2012), made during 1978–1992 bed by bed in the complete Breternitz Member of all available and suitable outcrops around Saalfeld.

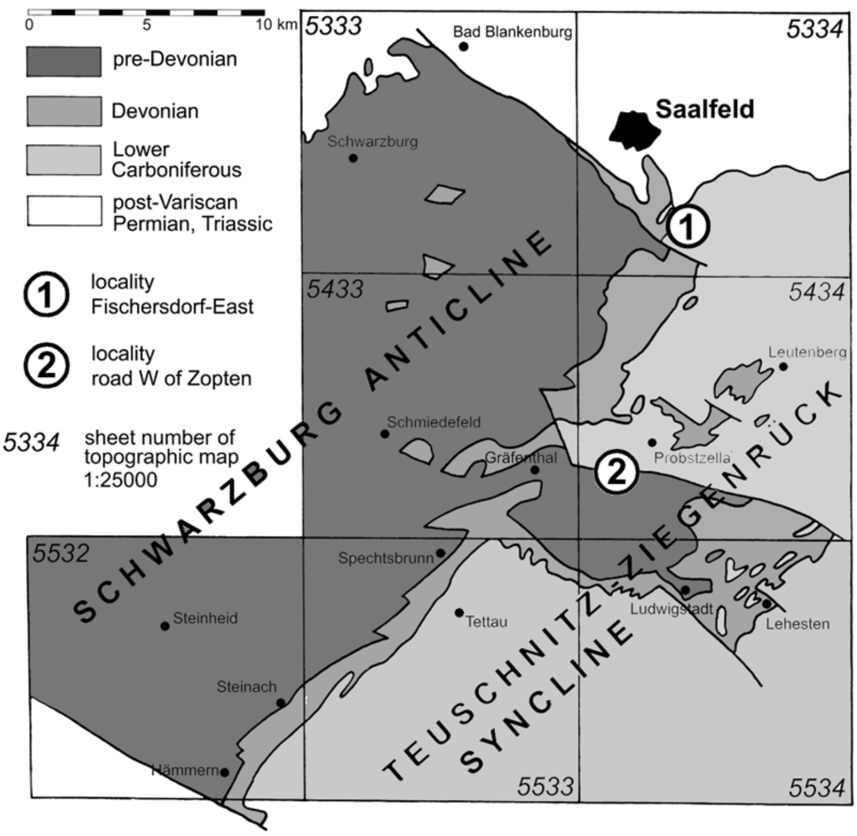

Fig. 14: Map of the western Thuringian Mts. south of Saalfeld where *Thurispina jogi* nov. sp. had been found.

Corals represent rare elements in the fauna of the *Wocklumeria* Genozone (upper Breternitz Member), though rather rich collections are now available after decades of intensive collecting. These started in 1947 by HEINZ PFEIFFER (1921–1994) for his monograph of the famous Bohlen section (1954), where he already registrated the presence of still undetermined Anthozoa in the Upper Devonian sequence – his fossils here used are stored in the Institute of Geology of the Technical University Bergakademie Freiberg. Today, the partly studied ahermatypic assemblage comprises at least:

Rugosa		
	>200 specimens	*Neaxon regulus* (RICHTER, 1848)
	1 specimen	*Neaxon bartzschi* WEYER, 1978
	1 specimen	*Petraia* cf. *decussata* MÜNSTER, 1839
	ca. 25 specimens	*Famennelasma* sp.
	ca. 20 specimens	*Cyathaxonia* (*Cyathocarinia*) *famenniana* FEDOROWSKI, 2003
	ca. 5 specimens	*Metriophyllum*? sp.
	1 specimen	*Guerichiphyllum*? *mirabile* WEYER, 2002
	1 specimen	*Gorizdronia* sp.
	7 specimens	*Thurispina jogi* nov. sp.
	2 specimens	*Famaxonia reuteri* WEYER, 1971
Tabulata		
	2 specimens	*Sutherlandia* sp.
	ca. 20 specimens	*Cladochonus* sp.
	1 specimen	*Palaeacis* sp.

(WEYER, 1971a, 1971b, 1878c, 1984b, 2002; KORN & WEYER, 2003; the *Cyathaxonia* renamed by FEDOROWSKI, 2003b was originally determined as *Cyathaxonia* (*Cyathocarinia*) *tuberculata* SOSHKINA 1928 in RÓŻKOWSKA, 1969: 56, and as *Cyathaxonia* (*Cyathocarinia*) n. sp. in WEYER, 1984b: 20, photo 4/4, 5.)

Subordo Plerophyllina SOKOLOV, 1960
Familia Plerophyllidae KOKER, 1924 / Pentaphyllidae SCHINDEWOLF, 1942
Subfamilia Anisophyllinae IVANOVSKIY, 1965

Thurispina nov. gen.

Name: from Thuringia and the trabicular spines.
Type species: *Thurispina jogi* nov. sp.

Diagnosis: Small solitary, plerophyllinoid, long conical, diaphragmatophorous Rugosa, at maturity ampleximorph with somewhat shortened major septa of nearly equal length and with extremely short free minor septa. Postcalice-ontogeny starts with aseptal prototheca, then the appearance of cardinal and antiseptum followed by a phase of six protosepta (antiseptum long, as in Polycoeliidae). In early middle stages with prominent protosepta, some metasepta and all catasepta are secondarily reduced during calice-ontogeny; later most metasepta remain active and demonstrate a tachylasmatoid trend (without clear pinnate arrangement), and the antiseptum starts to shorten. Septal microstructure coarsely trabicular (monacanth, adult diameter of spines 300–400 µm).

Discussion: A remarkable feature of the new genus is the unusual variation in the length of the antiseptum; therefore, some cross sections do not show the typical plerophyllid/pentaphyllid septal plan and temporarily imitate polycoeliids. This is unknown in the other trabicular taxa, here provisionally classified as Anisophyllinae. They all differ in additional criteria: *Oligophyllum* POČTA, 1902 has an extremely deep calice, no mature ampleximorph phase, and nearly no tabulae, just as *Anisophyllum* MILNE-EDWARDS & HAIME, 1850 with its rhopaloid three protosepta; *Pentaxon* GLINSKI, 1999 developed an aulos-like axial structure.

Occurrence: Monotypic in the uppermost Famennian (*Wocklumeria sphaeroides* Zone) of Saalfeld region, Thuringia, Germany.

Thurispina jogi nov. sp.
(Figs. 15/1–28, 16/1–12, 17/1–14, 18/1–18, 19/1–3, 20/1–34)

1984 – *Pentaphyllum*? n. sp. – WEYER: 20, fig. 4/6.
2008 – gen. nov. sp. nov. aff. *Hexalasma* SOSHKINA, 1928 – WEYER: 101, fig. 6/1–5.

Name: In old friendship dedicated to JÖRG („Jogi“) SCHNEIDER on occasion of his 65th birthday celebration.

Holotype: specimen no. FG-662/2, BA Freiberg (old numbers i10/51, C618), collection HEINZ PFEIFFER 1954 = 28 CS (26 P, 2 TS), 6 LS (P), 12 R. – figs. 15/1–28, 20/13–17.

Type locality, horizon: small ancient quarry (abandoned, now bus station) west of Fischersdorf southeast of Saalfeld; beds 32.6-10. of uppermost Breternitz Member, Gleitsch Formation, Saalfeld Group (*Wocklumeria sphaeroides* ammonoid Zone).

Paratypes: no. 2–5 collection KONRAD BARTZSCH 1954, from type locality and horizon.

1. no. FG-662/1, BA Freiberg (old numbers i10/41, C637), collection Heinz PFEIFFER 1954 = 25 CS (23 P, 2 TS, numbered from distal to proximal), 4 R. – figs. 16/1–22, 20/9. There are 4 additional CS (3 P, 1 TS, numbered 26–29) of the basal *Metriophyllum*? sp., which includes the sections 12–29.
2. no. MB.K.188.1. (old number C504) = 21 CS (14 P, 7 TS), 5 R. – figs. 17/1–14, 20/1–8.
3. no. MB.K.188.2. (old number C483) = 5 CS (P), 5 R. – fig. 18/16–18.
4. no. MB.K.188.3. (old number Fi4) = 10 CS(5 P, 5 TS), 3 LS (TS), 1 R. – fig. 18/1–12, 20/18–23.
5. no. MB.K.188.4. (old number Fi6) = 4 CS (2 P, 2 TS), 2 LS (1 P, 1 TS), 1 R. – fig. 18/13–15, 20/11–12.
6. no. MB.K.185. (old number C818), unknown collector ca. 1880 (? Ernst ZIMMERMANN (1860-1944), road above village Zopten east of Gräfenthal, upper Breternitz Member (*Wocklumeria* Genozone, perhaps also *Wocklumeria sphaeroides* Zone as the holotype) = 7 CS (5 P, 2 TS), 6 R. – figs. 19/1–3, 20/10.

Diagnosis: Identical with the generic one up to the future discovery of a second species.

Description: Long-conical corals of 30–40 mm length and 12–15 mm calice diameter, fixed by a large talon, straight or slightly cornute (cardinal septum on concave side or lateral); the non-adult specimen of fig. 20/9 measures 23 mm in length and 11 mm in distal diameter. Archaeotheca only with fine transverse growth lines or (fig. 20/9) also with very weak longitudinal septal furrows. Rejuvenescense observed twice (fig. 15/28, 17/14). Adult 40–46 septa, arranged according to the following formulae (n = number of major septa, N = number of all septa):

$\begin{array}{c\|c}3&4\\\hline 7&6\end{array}$	n24, N40 fig. 15/23
$\begin{array}{c\|c}3&3\\\hline 7&7\end{array}$	n24, N41 fig. 18/13
$\begin{array}{c\|c}5&5\\\hline 6&4\end{array}$	n24, N41 fig. 17/11
$\begin{array}{c\|c}5&4\\\hline 5&7\end{array}$	n25, N42 fig. 18/6
$\begin{array}{c\|c}5&4\\\hline 7&7\end{array}$	n27, N46 fig. 18/18

The mature calice stage is ampleximorph (figs. 15/21, 22, 18/13): thin major septa shortened, of equal length after loss of protoseptal prominence (unshortened cardinal septum situated in a weak lateral fossula, antiseptum not longer shorter than its neighbours); tiny free catasepta still active or already reduced at former calicular bases by stereoplasmatic thickening of the archaeotheca. Depth of calice up to double interior diameter (fig. 17/14). All septa are equally short near the upper calicular rim (fig. 17/13); the elongated growth of major septa starts a little deeper (figs. 17/12, 18/7), when the wall is already rather thick. Active hyposepta are observed in but one section (fig. 16/21) near the upper calicular margin.

Fig. 15. *Thurispina jogi* n. sp., holotype no. FG-662/2, uppermost Famennian (upper *Wocklumeria* Genozone, *Wocklumeria sphaeroides* Zone), uppermost Breternitz Member of Gleitsch Formation (beds 32.6-10.), locality Fischersdorf-East SE of Saalfeld, collection HEINZ PFEIFFER 1954.
1 to 2 – cross sections of aseptal prototheca stage (no. 1, 2), x 7, fixed by a large talon using a dead Rugosa coral as hardground; 3 to 7 – subtabular cross sections (no. 3–7) with mainly 6 active, partly prominent protosepta, x 5, cardinal and antiseptum long, metasepta reduced (hidden within the thickened archaeotheca); 8 to 13 – subtabular cross sections (no. 9–14), x 5, with mostly prominent protosepta and sometimes first active tiny metasepta, antiseptum always long, tabulae grey (8–10); 14 to 19 – subtabular cross sections (no. 15–17, 19–21), x 4.5, with six dominant protosepta and not pinnately arranged metasepta (antiseptum starts shortening in18–19, a first active cataseptum "appears" in 19), contrast between internal base-calice-picture and top-calice-picture (hidden in the external wall) is remarkably strong (in sections 16–17 only intern 14 major septa are left after septal reduction from 21 major septa and 13 catasepta already present in these levels during their times as former upper calicular rims); 20, 21 – subtabular cross sections (no. 22, 26), x 4, with brevisepta (mature amplexoid trend) and more numerous, still active catasepta; 22 – ampleximorph cross section (no. 27), x 4, at calicular base (subtabular regions white); 23 – lower calicular cross section (no. 28), x 4, ampleximorph, with all 40 major and minor septa active, weak lateral cardinal fossula; 24 – upper calicular cross section (no. 33), x 4, with rejuvenescense; 25 – subtabular median longitudinal section (no. 23), x 4; 26, 27 – lower calicular tangential longitudinal sections (no. 30, 31), x 8, with trabicular spines; 28 – sketch of corallum, x 1.5, indicating the position of the prepared sections (dotted line at base of calice).

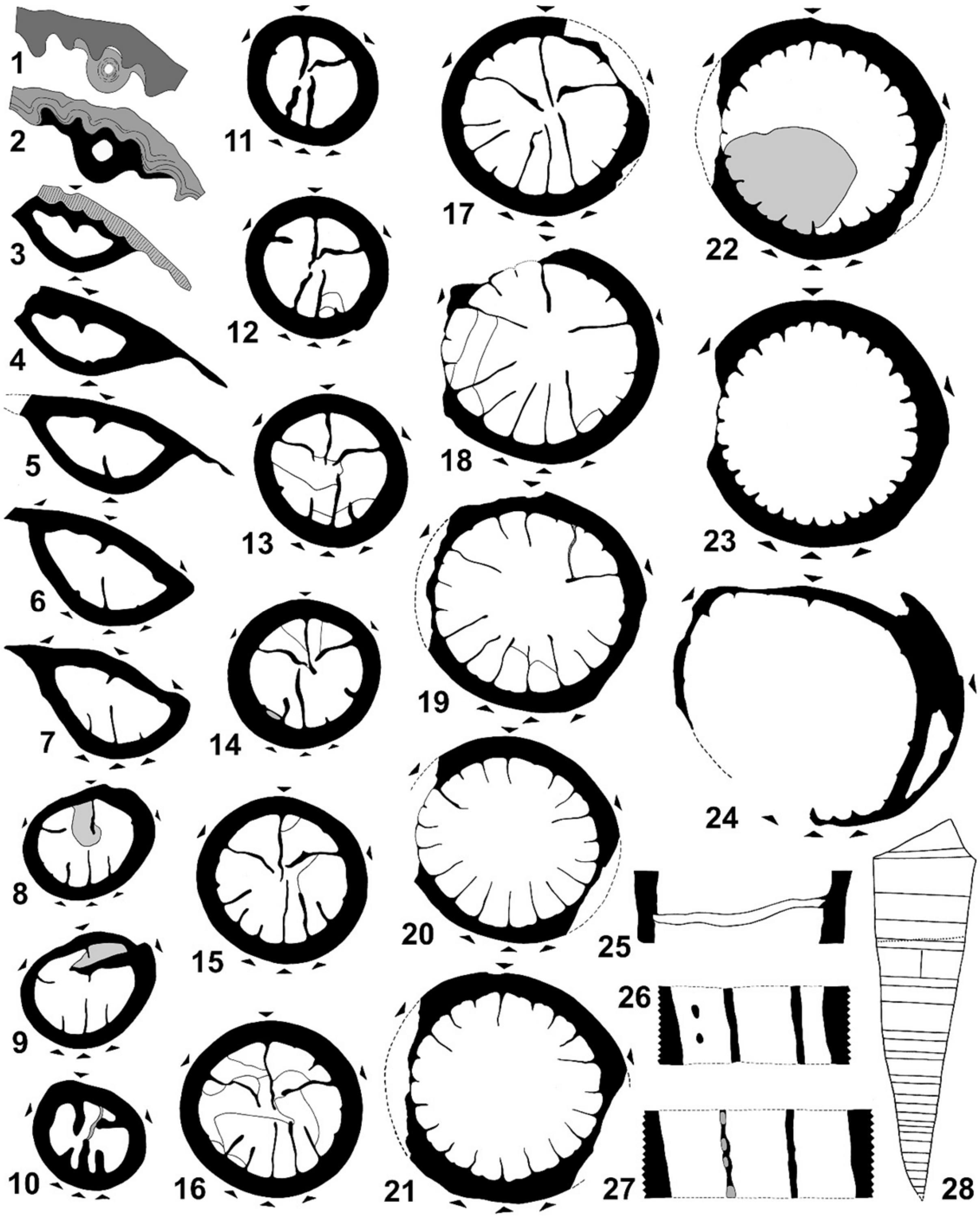
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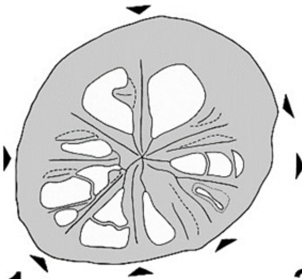
Fig. 16: *Thurispina jogi* n. sp., paratype no. FG-662/1, BA Freiberg, uppermost Famennian (upper *Wocklumeria* Genozone, *Wocklumeria sphaeroides* Zone), uppermost Breternitz Member of Gleitsch Formation (beds 32.6-10.), locality Fischersdorf-East SE of Saalfeld, collection Heinz Pfeiffer 1954.

The specimen (4–21) had externally overgrown a *Metriophyllum*? sp. (1–14), which differs from the Frasnian type species *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850 in the absence of an antiseptal catasepta triad.

Such taxa are similar to Late Famennian corals determined by Różkowska (1969: 34, 37) as *Metriophyllum* aff. *bouchardi* Milne-Edwards & Haime, 1850 (renamed *Metriophyllum rozkowskae* Fedorowski, 2003) and as "*Metriophyllum soshkinae* Różkowska, 1969"; they represent another genus. The latter name is invalid: it was introduced as a replacement name for the Artinskian *Lopholasma gracile* Soshkina, 1928, a supposed homonym of the Eifelian *Metriophyllum gracile* Schlüter, 1884, because in those days *Lopholasma* Simpson, 1900 was treated as a synonym of *Metriophyllum* Milne-Edwards & Haime, 1850. Then the type of the nomen novum automatically – according to the International Code of Zoological Nomenclature – becomes that of the replaced Russian Permian species, not the Polish Famennian material, as indicated by Różkowska. Meanwhile (Weyer, 1994: 195, 1996: 86, 1997: 45), *Lopholasma* as junior synonym of *Lindstroemia* Nicholson & Thomson, 1876 differs from the related *Metriophyllum* in the calicular shortening of its cardinal septum. The never revised *Lopholasma gracile* Soshkina, 1928 remains indeterminable with the published data.

1 to 12 – main cross sections of *Metriophyllum*? sp. (no. 29–16, oriented with their antiseptum down; no. 26 and 21 not drawn), bearing the externally attached *Thurispina jogi* (antiseptum in NW), which in 9–12 started fixing by a root-like outgrowth also inside the calice of the dead *Metriophyllum*? sp. (black: skeleton, white: subtabular hollow space, grey: stereoplasma); white free spaces directly between the two corals in 8–14 have sediment filling; subtabular regions white in 4, grey in 5–7; prototheca in 4–7, phase with six protosepta (antiseptum long) in 10–12 (base-calice-pictures, indicating the reduction of metasepta and catasepta), x 10 (1–4), x 8 (5–7) and x 7 (8–12); 13 to 20 – main cross sections of *Thurispina jogi* (no. 14, 12–7, 5), subtabular (13–16) and calicular (19–20), calicular parts in 17–18 grey; overgrown parts of the upper calicular rim of the *Metriophyllum*? sp. still visible in 13–14, x 7 (13–15), x 6 (16, 17), x 5 (18, 19), and x 3.5 (20); 21 – septal detail (right cardinal quadrant, lateral septum to the left) of 20, x 10, with still active three catasepta and three hyposepta in the upper calice; 22 – sketch of the two corals indicating the position of the 29 prepared cross sections, x 1.5 (stippled line in the middle marks the calicular base).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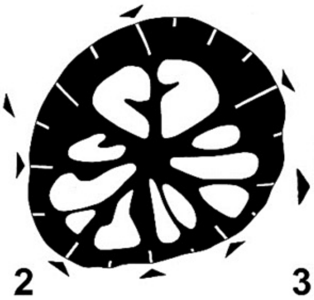
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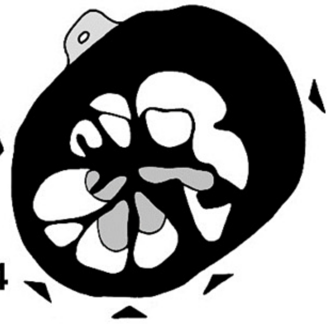
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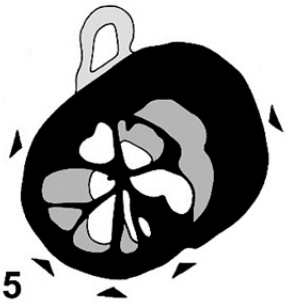
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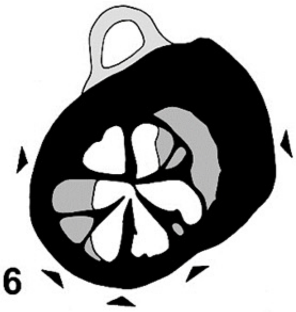
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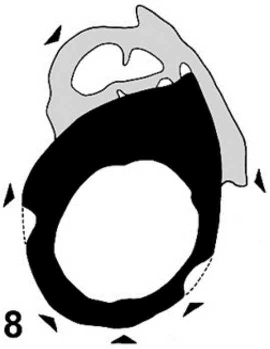
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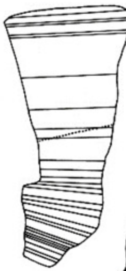
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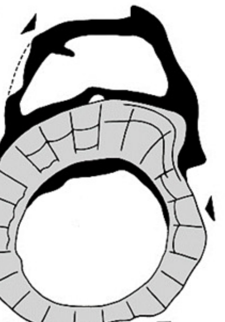
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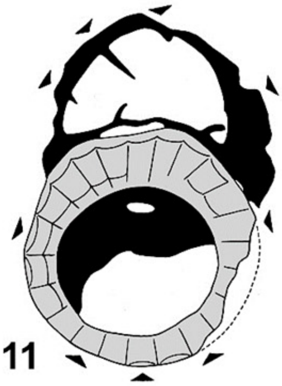
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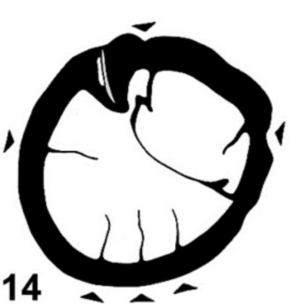
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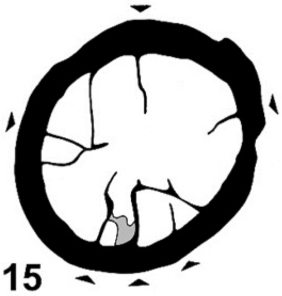
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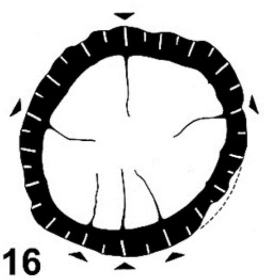
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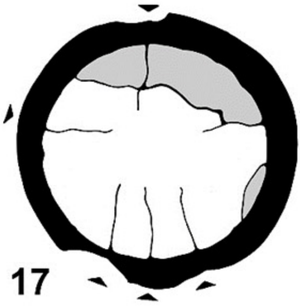
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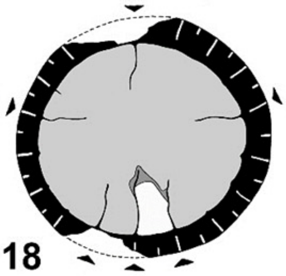
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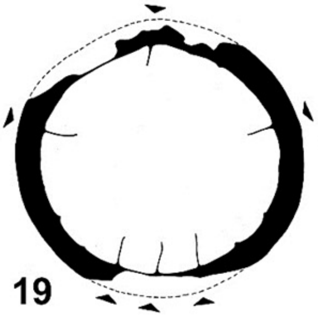
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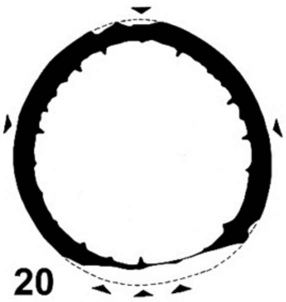
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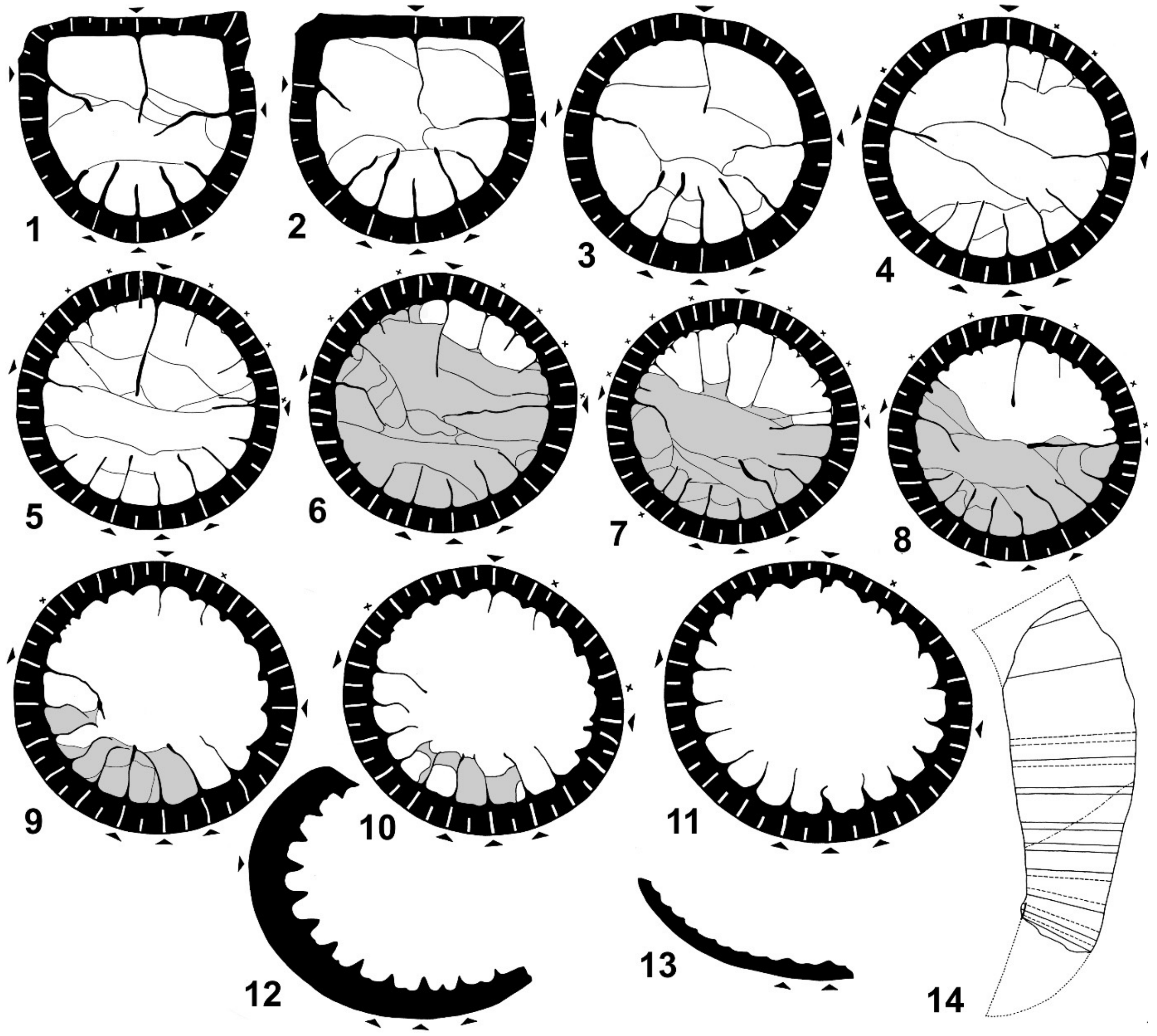
Fig. 17: *Thurispina jogi* n. sp., paratype no. MB.K.188.1., uppermost Famennian (upper *Wocklumeria* Genozone, *Wocklumeria sphaeroides* Zone), uppermost Breternitz Member of Gleitsch Formation (beds 32.6-10.), locality Fischersdorf-East SE of Saalfeld, collection KONRAD BARTZSCH 1954.

1 to 5 – subtabular cross sections (no. 1, 3, 5, 8, 9), x 5 (1–3), x 4.5 (4), and x 4 (5), anomalous carinae-like "septa" in cataseptal position (in 4–11) externally marked by crosses, antiseptum shortened, tabulae always (in 1–10) drawn as thin basal line; 6 to 10 – cross sections of the oblique calicular base (no. 6–10. subtabular regions grey), x 4 (6) and x 3.5 (7–10), without active catasepta; 11 to 13 – calicular cross sections (no. 16, 20, 21), x 3.5 (11) and x 3 (12, 13); 14 – sketch of corallum indicating the position of the prepared cross sections (full lines = drawings, dotted lines = not illustrated; oblique dotted line = base of calice, parallel to upper calicular rim), x 1.5 (first dotted line = no. 17+18) – see photos figs. 20/1–8.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The postcalyx-ontogeny begins with an aseptal prototheca, well-preserved in two specimens (figs. 15/1, 2, 16/4–7), where the planctonic larvae had settled (with an extended talon) on a necessary hardground using the interior calice wall of a dead *Neaxonella*? sp. (fig. 15) or the external wall of a *Metriophyllum*? sp. (fig. 16) – thus the earliest skeleton was protected and not destroyed during fossilisation or diagenesis. The following phase with six protosepta (figs. 15/3–12) has at first a long cardinal and antiseptum (reminiscent of an uncompleted axial septum), later sometimes nearly reaching the axis and always of polycoeliid appearance (antiseptum never shortened). During the next growth stage (figs. 15/12–17), short or longer metasepta are partially developed (without the pinnate arrangement according to the insertion sequence: first tachylasmatoid trend) – in reality they all were regularly present, but some of them became secondarily reduced at former calice bases (figs. 16/18, 18/16). The plerophyllid/pentaphyllid shortening of the antiseptum can start here (figs. 17/1, 18/1) or later (fig. 15/19), but sometimes it is even missing (fig. 16/17–19, 18/16) or disappears again (fig. 19/1–3). The last period before the adult ampleximorph morphology (figs. 15/18–20) shows the complete set of metasepta; septal reduction had stopped. One not adult specimen presents a calice with six prominent thin protosepta (fig. 16).

The simple tabulae are horizontal or appear weakly domed (small zone of downward bending near the wall). Their orientation follows the external rugae in specimens with straight growth, but is oblique to these growth lines in a cornute corallum (fig. 17/14) – there tabulae run parallel to the corresponding upper calicular margin (WEYER, 1973b: 700, fig. 4, 5). Sometimes a weak fossula is visible, both lateral (figs. 18/5–7) and tabular (fig. 18/13).

The septal microstructure is coarsely trabicular (monacanth), as seen in cross and longitudinal sections, and best in an artificial cast (fig. 20/6); diameter of trabicular spines at distal septal margins 300–400 µm.

Fig. 18: *Thurispina jogi* n. sp., uppermost Famennian (upper *Wocklumeria* Genozone, *Wocklumeria sphaeroides* Zone), uppermost Breternitz Member of Gleitsch Formation (beds 32.6-10.), locality Fischersdorf-East SE of Saalfeld, collection KONRAD BARTZSCH 1954.
1 to 12 – paratype no. MB.K.188.3.; 1 to 4 – subtabular cross sections (no. 1, 2, 4, 5), x 5 (1, 2), x 4 (3) and x 3.5 (4), nearly all with reduced catasepta, length of antiseptum variable (left lateral septum in 1 broken, originally long); 5 to 7 – calicular cross sections (no. 6, 7, 9), x 3.5 (5, 6) and x 3 (7), with lateral cardinal fossula, catasepta active in upper calice (6, 7) and starting to become reduced in lower calice (5); 8 – subtabular median longitudinal section (no. 3), x 4; 9 – tangential longitudinal section in upper calice (no. 11), x 4, with trabicular spines; 10 – part of upper calicular cross section (no. 12), x 8, with trabicular septal microstructure inside the wall; 11 – median longitudinal section in upper calice (no. 10), x 4, with rather coarse trabicular spines; 12 – sketch of corallum indicating the position of the prepared sections, x 1.5 (photos see figs. 20/18–23). 13 to 15 – paratype no. MB.K.188.4.; 13 – cross section near calicular base (no. 4), x 5, subtabular regions white (tabulae drawn only as thin basal line), antiseptum as long as its neighbours, catasepta rarely seen active (mostly reduced within the thick wall); 14 – tangential longitudinal section with base of calice (no. 5), x 5, right septum mostly within the wall is the trabicular left antilateral protoseptum, smaller septum within the left wall is a trabicular cataseptum – see photos figs. 20/11, 12. 16 to 18 – paratype no. MB.K.188.2., 3 calicular cross sections (no. 3–5), x 5 (16, 17) and x 3.5 (18), with antiseptum as long as its neighbours, catasepta active in upper calice (18), mostly secondarily hidden within the archaeotheca in deeper calice (16, excepting left of antiseptum, and 17, excepting left lateral septum).


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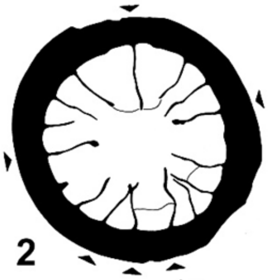
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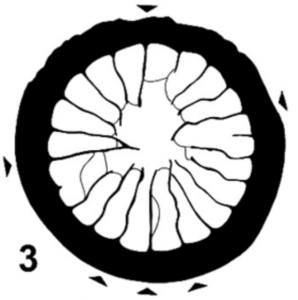
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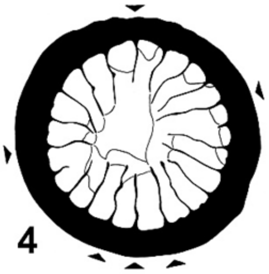
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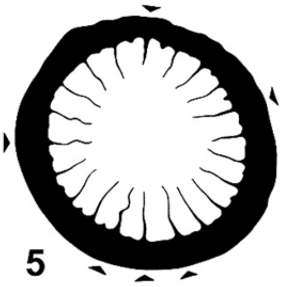
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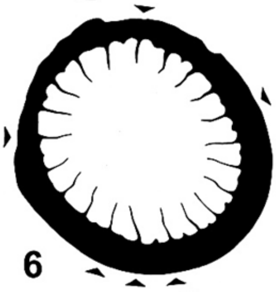
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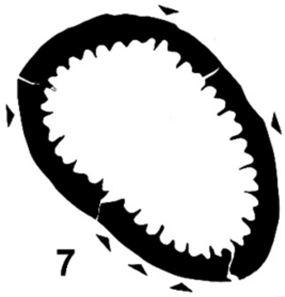
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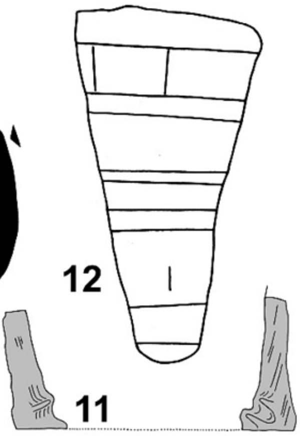
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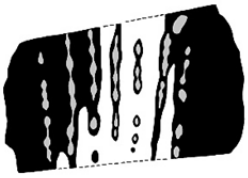
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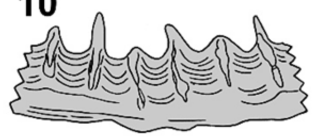
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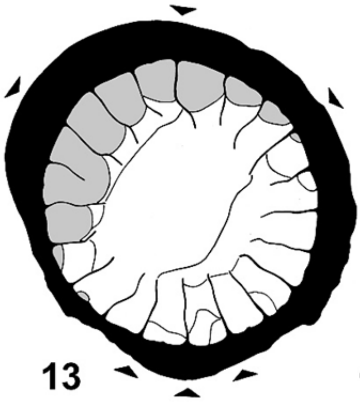
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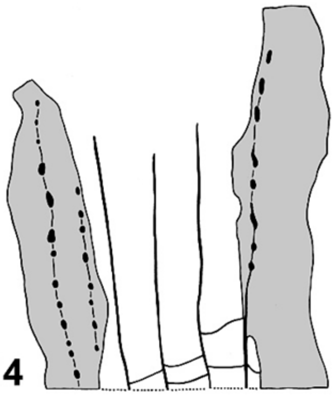
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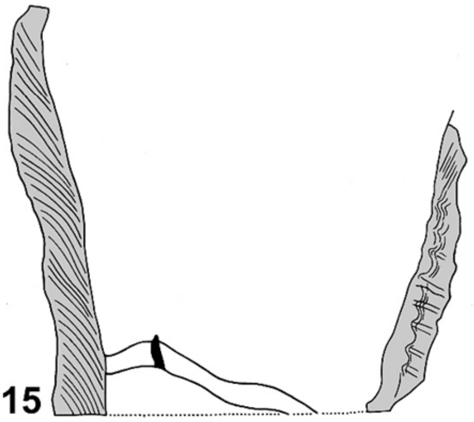
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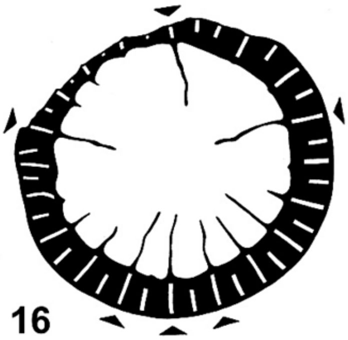
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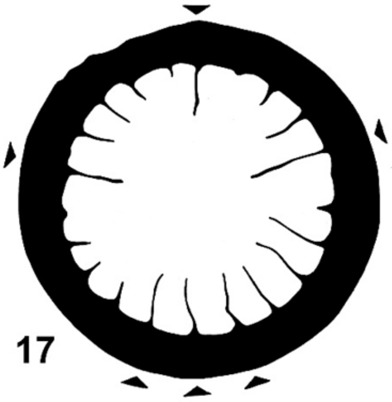
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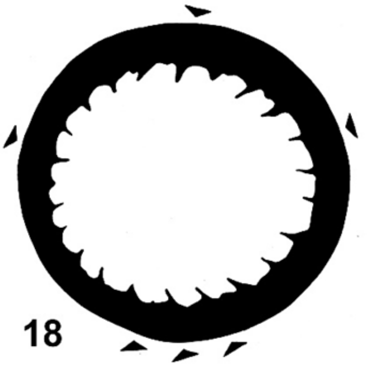
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Discussion: One paratype (fig. 17) has some strange thin "septa" or probably better "carinae" in cataseptal positions of calicular and subtabular regions, rather long in comparison with the neighbouring true septa, and especially marked in the drawings. The feature is not known from further Rugosa and perhaps might be an anomaly.

The section of fig. 15/24 is untypical with its few active septa in the upper calice. Obviously, this is due to the rejuvenescense, as all other specimens did not reduce some of their septa in such a level near to the upper calicular rim.

The ontogeny of the new species demonstrates that the classical taxonomic boundary between Polycoeliidae and Plerophyllidae/Pentaphyllidae (SCHINDEWOLF, 1942) is not as sharp as generally assumed. This was already indicated by ILJINA (1984) in the case of *Hexalasma* SOSHKINA, 1928 (see fig. 12, 13). SCHINDEWOLF (1942) would have spoken of a pentaphylloid or "tetraphylloid" ontogenetic mode; sensu FEDOROWSKI (2009a) it would be no longer a "cryptophylloid" mode, but a variant of the common zaphrentoidid mode.

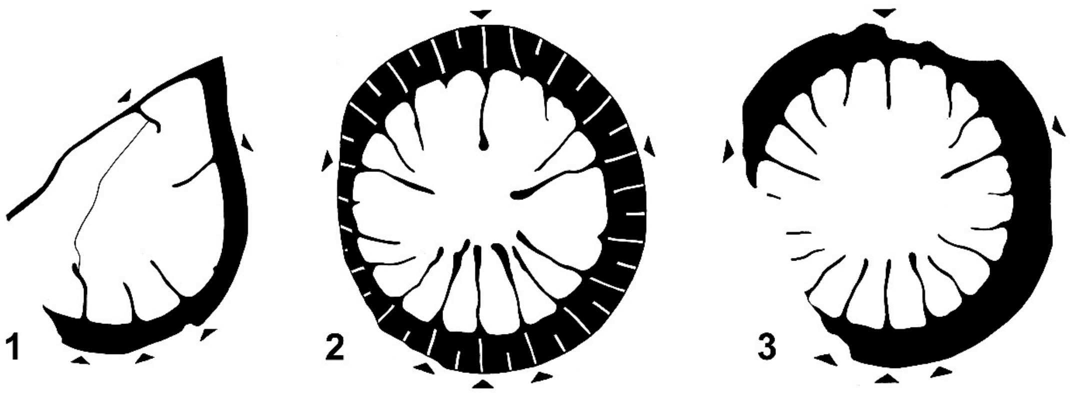

Fig. 19: *Thurispina jogi* n. sp., paratype no. MB.K.185., uppermost Famennian (probably upper *Wocklumeria* Genozone), upper Breternitz Member of Gleitsch Formation, road ca. 1 km W of village Zopten (W of Probstzella), unknown collection of end 19th century.

1 – subtabular cross section (no. 6), x 8, with 6 prominent protosepta (antiseptum already shortened) and first metaseptum in right antiquadrant; 2, 3 – calicular cross sections (no. 3,1), x 6, with dominant pinnate arrangement of metasepta and first tachlasmatoid trend (*sensu* HUDSON, 1936) – first metaseptum shorter than the second one in right antiquadrant, catasepta at first secondarily hidden within the archaeotheca (2, see photo pl. 20/10), later (3) sometimes still visible inside the wall.

Fig. 20: *Thurispina jogi* n. sp., uppermost Famennian (upper *Wocklumeria* Genozone).

1 to 8 – paratype no. MB.K.188.1., *Wocklumeria sphaeroides* Zone, uppermost Breternitz Member of Gleitsch Formation (beds 32.6-10.), locality Fischersdorf-East SE of Saalfeld, collection KONRAD BARTZSCH 1954. 1, 2 – exterior side views, x 1.5; 3, 4 – subtabular cross sections (no. 1, 5), x 6 and x 5; 5 – calicular cross section (no. 19), x 3; 6 – artificial cast (prepared with HCl) of upper calicular part, x 5, with coarse trabiculae of metasepta and catasepta; 7, 8 – trabicular microstructure in cross sections (no. 17, 18), x 8 – see fig. 17/1–14.

9 – paratype no. FG-662/1, BA Freiberg, same locality and horizon, collection HEINZ PFEIFFER 1954. exterior side view, x 2 – see fig. 16/1–22. 10 – paratype no. MB.K.185., probably upper *Wocklumeria* Genozone), upper Breternitz Member of Gleitsch Formation, road ca. 1 km W of village Zopten (W of Probstzella), unknown collection of end 19th century. Calicular cross section (no. 3), x6 – see Fig. 19/1–3. 11 to 12 – paratype no. MB.K.188.4.; same locality, horizon and collection as 1–8. 11 – exterior side view, x 1.5; 12 – subtabular cross section (no. 3), x 5 – see fig. 18/13–15. 13 to 17 – holotype no. FG-662/2, same locality, horizon and collection as 9. Early ontogenetic subtabular cross sections (no. 3, 7, 9, 12, 16), x 8 (13–16) and x 6 (16) – see fig. 15/1–28. 18–23. paratype no. MB.K.188.3.; same locality, horizon and collection as 1–8. 18 – exterior side view, x 1.5; 19 – early cross section (no. 1), x 8; 20 – subtabular longitudinal section, x 5; 21, 22 – subtabular cross sections (no. 4, 5), x 5 and x 3.7; 23 – basal calicular cross section (no. 6), x 4 – see fig. 18/1–12.


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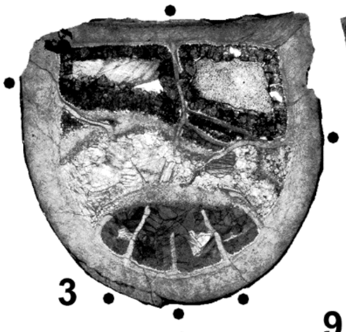
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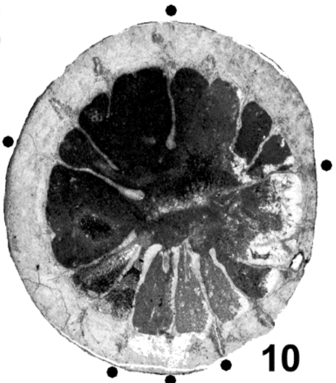
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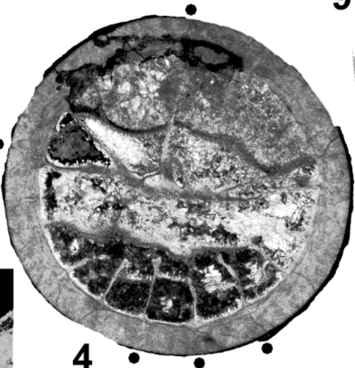
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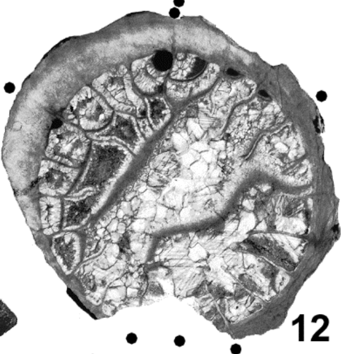
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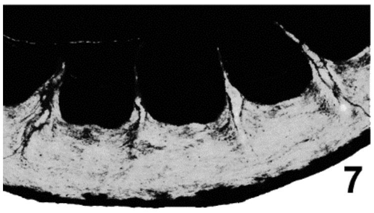
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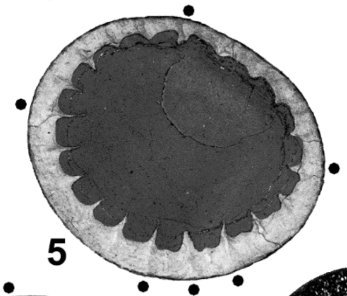
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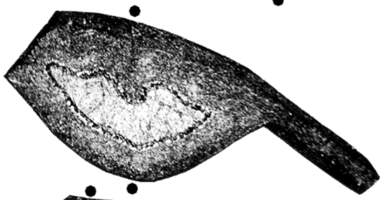
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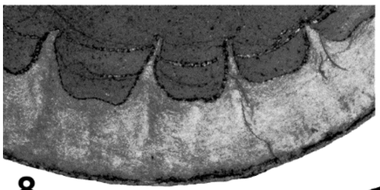
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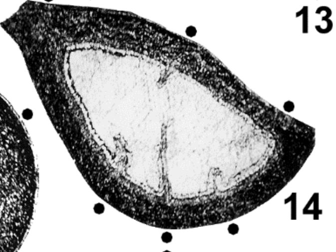
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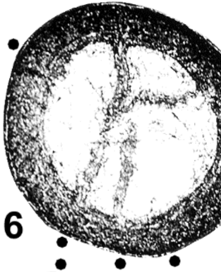
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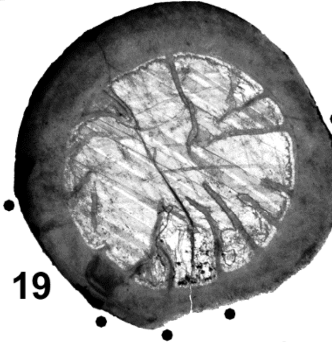
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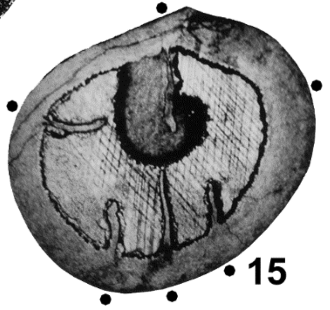
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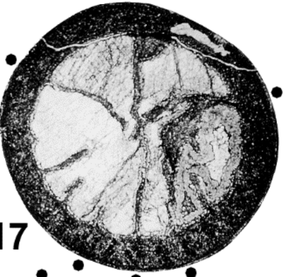
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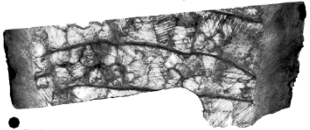
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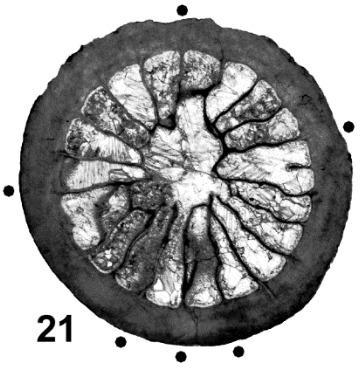
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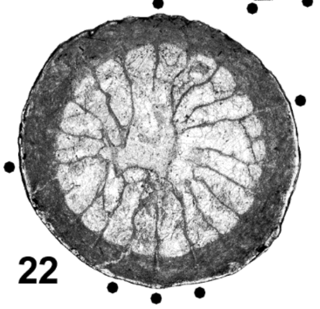
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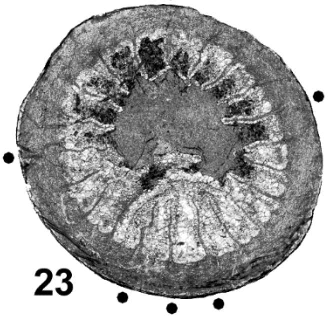
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Acknowledgements

My sincere thanks for their kind help go to KONRAD BARTZSCH, Saalfeld (who collected long ago in 1954 most specimens of the rare new genus), to BIRGIT GAITZSCH and JÖRG W. SCHNEIDER, Freiberg (for the loan of specimens under their care, of the PFEIFFER collection from the Famennian of Saalfeld), to ANGELA EHLING and WOLFGANG LINDERT, Berlin (for the loan of specimens from the collection of SCHINDEWOLF 1942), to OLGA Leonidovna KOSSOVAYA, St.-Peterburg (for the *Hexalasma* photographs from the collection of SOSHKINA 1928), and to EWA RONIEWICZ, Warszawa (for many discussions on Scleractinian microstructures).

References

ALLOITEAU, J. (1952): Madréporaires post-paléozoiques. – In: PIVETEAU, J., Traité de Paléontologie, 1: 530–584; Paris (Masson).

AMSDEN, T.W. (1949): Stratigraphy and Paleontology of the Brownsport Formation (Silurian) of Western Tennessee. – Bulletin, Peabody Museum of Natural History, Yale University (New Haven, Connecticut), 5: 1–138.

ARTHABER, G.v. (1900): Das jüngere Paläozoicum aus der Araxes-Enge bei Djulfa. – In FRECH, F. & ARTHABER, G.v.: Über das Paläozoicum in Hocharmenien und Persien. – Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orient (Wien, Leipzig), 12(4): 209–302.

BAARS, C., POUR, M.G. & ATWOOD, R.C. (2012): The earliest rugose coral. – Geological Magazine (Cambridge), 150(2): 371–380.

BARTZSCH, K. & WEYER, D. (2012): Zur Stratigraphie des Breternitz-Members (Obere Clymenien-Schichten, Oberdevon) von Saalfeld (Schwarzburg-Antiklinorium, Thüringisches Schiefergebirge). – Paläontologie, Stratigraphie, Fazies (20), Freiberger Forschungshefte, C 542: 1–54.

BECKER, R.T., JANSEN, U., PLODOWSKI, G., SCHINDLER, E., ABOUSSALAM, Z.S. & WEDDIGE, K. (2004a): Devonian litho- and biostratigraphy of the Dra Valley area. An overview. – In: EL HASSANI, A. (ed.), Devonian neritic-pelagic correlation and events in the Dra Valley (Western Anti-Atlas, Morocco). Fieldtrip Guidebook, International Meeting on Stratigraphy, Rabat, March 1–10, 2004. – Documents de l´Institut Scientifique, Université Mohammed V, Agdal, Rabat, 19: 3–18.

BECKER, R.T., BOCKWINKEL, J., EBBIGHAUSEN, V., ABOUSSALAM, Z.S., EL HASSANI, A. & NÜBEL, H. (2004c): Lower and Middle Devonian stratigraphy and faunas at Bou Tserfine near Assa (Dra Valley, SW Morocco). – In: EL HASSANI, A. (ed.), Devonian neritic-pelagic correlation and events in the Dra Valley (Western Anti-Atlas, Morocco). Fieldtrip Guidebook, International Meeting on Stratigraphy, Rabat, March 1–10, 2004. – Documents de l´Institut Scientifique, Université Mohammed V, Agdal, Rabat, 19: 90–100.

BECKER, R.T., ABOUSSALAM, Z.S., BOCKWINKEL, J., EBBIGHAUSEN, V., EL HASSANI, A. & NÜBEL, H. (2004b): Upper Emsian stratigraphy at Rich Tamelougou near Torkoz (SW Dra Valley, Morocco). – In: EL HASSANI, A. (ed.), Devonian neritic-pelagic correlation and events in the Dra Valley (Western Anti-Atlas, Morocco). Fieldtrip Guidebook, International Meeting on Stratigraphy, Rabat, March 1–10, 2004. – Documents de l'Institut Scientifique, Université Mohammed V, Agdal, Rabat, 19: 85–89.

BENTON, M.J. (1979): H. A. Nicholson (1844–1899): pioneer of thin section taxonomy. – Fossil Cnidaria (Newsletter, International Association for the Study of Fossil Cnidaria) (Washington), 8(2): 17–24.

BERKOWSKI, B. (2008): Emsian deep-water Rugosa assemblages of Hamar Laghdad (Devonian, Anti-Atlas, Morocco). – Palaeontographica (Stuttgart), A 284 (1–3): 17–68.

BERKOWSKI, B. & WEYER, D. (2012): *Hamaraxonia*, a new pseudocolumellate genus of Middle Devonian deep-water Rugosa (Anthozoa) from Morocco. – Geologica Belgica (Bruxelles), 15(4): 245–253.

BERNARD, H.M. (1904): The Prototheca of the Madreporaria, with Special Reference to the Genera *Calostylis*, Linds., and *Moseleya*, Quelch. – The Annals and Magazine of Natural History (London), series 7, 13(73): 1–33.

BROWN, T.C. (1909): Studies on the Morphology and Development of Certain Rugose Corals. – Annals of the New York Academy of Sciences, 19(1, 3): 45–97.

CARRUTHERS, R.G. (1919): A Remarkable Carboniferous Coral. – The Geological Magazine (London), new series, decade 6, 6(10) [= whole series, 56(10)]: 436–441.

CHEVALIER, J.P. (1961): Recherches sur les Madréporaires et les formations récifales miocènes de la Méditerranée occidentale. – Mémoire de la Société Géologique de France (Paris), nouvelle série, 40(93): 1–562.

CHI, YUNGSHEN S. (1937): On some Simple Corals from the Permian of Yungsin, Kiangsi. – Bulletin of the Geological Society of China (Nanking), 17(1): 83–109.

DEJEAN, P.F.M.A. (1821): Catalogue de la Collection de Coléoptères de M. le Baron Dejean. – I–VIII: 1–136; Paris.

DYBOWSKI, W. (1873–1874): Monographie der Zoantharia sclerodermata rugosa aus der Silurformation Estlands, Nord-Livlands und der Insel Gotland, nebst einer Synopsis aller palaeozoischen Gattungen dieser Abtheilung und einer Synonymik der dazu gehörigen, bereits bekannten Arten. – Archiv für die Naturkunde Liv-, Ehst- und Kurlands (Dorpat), Serie 1, 5 (3, 4): 257–532 [1873: 257–414, pls. 1–2; 1874: 415–532, pls. 3–5].

EASTON, W.H. (1944): Corals from the Chouteau and related formations of the Mississippi Valley region. – Report of Investigation, State of Illinois, Division of the State Geological Survey (Urbana/Illinois), 97: 1–93.

EHRENBERG, C.G. (1834): Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche der physiologischen Systematik derselben. – Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, 1832 (1), Physikalische Abhandlungen: 225–380.

EICHWALD, C.E. von (1860): Lethaea Rossica ou Paléontologie de la Russie. I. Ancienne Periode. – I–XIX, 17–26, 1–681, 682–1657 (2 vols.), Atlas (1–8, 59 pls.); Stuttgart (E. Schweizerbart).

EL HASSANI, A., ed. (2004): Devonian neritic-pelagic correlation and events in the Dra Valley (Western Anti-Atlas, Morocco). [Fieldtrip Guidebook,] International Meeting on Stratigraphy [IUGS Subcommission on Devonian Stratigraphy], Rabat, March 1–10, 2004. – Documents de l'Institut Scientifique, Université Mohammed V, Agdal, Rabat, 19: 1–139 (or 1–100). [there exist two seemingly identical editions with different pagination and text passages: a first "preprint-like" one available during the field meeting, and a second one published much later, but curiously without any declaration of being a distinctly altered, no longer the same publication, with many corrections of former mistakes].

FAN YING-NIAN (1978): Rugosa. – In: Atlas of Fossils of Southwest China, Sichuan Volume. 2. Carboniferous-Mesozoic. (ed.: Southwest China Institute of Geology). – 149–210, 620–631, pls. 50–76; Beijing (Geological Publishing House) (in Chinese).

FEDOROWSKI, J. (1974): The Upper Palaeozoic tetracoral genera *Lophophyllidium* and *Timorphyllum*. – Palaeontology (London), 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 (Stuttgart), A 191(4–6): 173–227.

FEDOROWSKI, J. (1991): Principles of early ontogeny in the rugose corals: a critical review. – Hydrobiologia (Dordrecht), 216/217: 413–418.

FEDOROWSKI, J. (1997): Remarks on the palaeobiology of Rugosa. – Geologos (Poznan, Wroclaw), 2: 5–58.

FEDOROWSKI, J. (2003a): Some remarks on diagenesis of rugose coral skeletons. – Geologos (Poznan, Wroclaw), 6: 89–109.

FEDOROWSKI, Jl (2003b): 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; 2 vols.: 49–124, 796–808, tab. 4, pls. 14–66; Warszawa (in Polish).

FEDOROWSKI, J. (2004): Considerations on most Rugosa and the Dividocorallia from de Groot's (1963) collection. – Scripta Geologica (Leiden), 127: 71–311.

FEDOROWSKI, J. (2009a: Revision of *Pentaphyllum* de KONINCK, 1872 (Anthozoa, Rugosa). – Palaeontology (London), 52(3): 569–591.

FEDOROWSKI, J. (2009b): Morphogenesis and taxonomic value of the circumaxial skeleton in Rugosa (Anthozoa). – Lethaia (Oslo), 42(2): 232–247.

FEDOROWSKI, J. (2010): Remarks on rugose coral taxonomy. – Palaeoworld (Amsterdam etc.: Elsevier), 19(3–4): 242–248.

FEDOROWSKI, J. (2012a): The new Upper Serpukhovian genus *Zaphrufimia* and homeomorphism in some rugose corals. – Palaeontographica (Stuttgart), A 296 (5–6): 109–161.

FEDOROWSKI, J. (2012b): On three rugose coral genera from Serpukhovian strata in the Upper Silesian Coal Basin, Poland. – Acta Geologica Polonica (Warszawa), 62(1): 1–33.

FEDOROWSKI, J. & BAMBER, E. W. (2001): Guadalupian (Middle Permian) solitary rugose corals from the Degerböls and Trold Fiord formations, Ellesmere and Melville islands, Canadian Arctic Archipelago. – Acta Geologica Polonica (Warszawa), 51(1): 31–79.

FISCHER-BENZON, R.v. (1871): Mikroskopische Untersuchungen über die Structur der *Halysites*-Arten und einiger silurischer Gesteine aus den russischen Ostsee-Provinzen. – Abhandlungen auf dem Gebiete der Naturwissenschaften (Naturwissenschaftlicher Verein Hamburg), 5(2): 1–31.

GILL, G.A. (1977): Essai de regroupement des Stylines (Hexacoralliaires) d'après la morphologie des bords internes de leurs septes. – Mémoires du Bureau de Recherches Géologiques et Minières (Paris), 89 (Second international symposium on corals and fossil coral reefs, Paris September 1975): 283–295.

GLINSKI, A. (1999): Plerophyllina (Anthozoa, Rugosa) im Mitteldevon der Eifel (Rheinisches Schiefergebirge, Deutschland). – Senckenbergiana Lethaea (Frankfurt/Main), 79(1): 105–117.

GRABAU, A.W. (1922): Palaeozoic Corals of China. Part I. Tetraseptata. Introduction, and Petraiidae, Streptelasmaidae and Cyathaxonidae. – Palaeontologica Sinica (Peking), series B, 2(1): 1–76.

GRABAU, A.W. (1928): Palaeozoic Corals of China. Part I. Tetraseptata II. Second contribution to our knowledge of the Streptelasmoid Corals of China and Adjacent Territories. – Palaeontologica Sinica (Peking), series B, 2(2): 1–175.

HEHENWARTER, E. (1951): Ergänzungen zur Tabulatenfauna des Perm von Timor und zur Stellung des Genus *Trachypsammia* GERTH. – Palaeontographica (Stuttgart), Supplement, 4 (Beiträge zur Geologie von Niederländisch-Indien), 5(2): 59–93.

HILL, D. (1935): British Terminology for Rugose Corals. – The Geological Magazine (London), 72(11): 481–519.

HILL, D. (1936): The British Silurian Rugose Corals with Acanthine Septa. – Philosophical Transactions of the Royal Society of London, series B - Biological Sciences, 226 (no. 534): 189–217.

HILL, D. (1956): Rugosa, Heterocorallia. – In: MOORE, R.C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata: F233–327; New York (Geological Society of America), Lawrence/Kansas (University of Kansas Press).

HILL, D. (1981): Rugosa and Tabulata. – In: TEICHERT, C. (ed.), Treatise on Invertebrate Paleontology, Part F, Coelenterata, Supplement 1: 1–762 (2 volumes), 462 figs.; Boulder/Colorado (Geological Society of America), Lawrence/Kansas (University Press).

HINDE, G. J. (1890): Notes on the Palaeontology of Western Australia. 2. Corals and Polyzoa. – The Geological Magazine (London), new series, decade 3, 7(5): 194–204.

HUANG JI-QING (1932): Permian Corals of Southern China. – Palaeontologia Sinica (Peiping), series B, 8(2): 1–163.

HUDSON, R.G.S. (1936): On the Lower Carboniferous Corals: *Rhopalolasma*, gen. nov. and *Cryptophyllum*, Carr. – Proceedings of the Yorkshire Geological Society (Wakefield), 23(2): 91–102.

ILJINA, T.G. (1965): Chetyrekhluchevye korally pozdney permi i rannego triasa Zakavkaz'ya. [Tetracorals of Late Permian and Early Triassic of the Transcaucasus]. – Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR (Moskva), 107: 1–104 (in Russian).

ILJINA, T.G. (1978): Reviziya roda *Anisophyllum* (Rugosa) [Revision of the rugose genus *Anisophyllum*]. – Paleontologicheskiy Zhurnal (Moskva), 1978 (3): 31–38 (in Russian).

ILJINA, T.G. (1980): Morfogenez septal'nogo apparata politseliin [Morphogenesis of the septal apparatus of Polycoeliina]. – In: SOKOLOV, B.S. (ed.), Korally i rify fanerozoya SSSR (Trudy 4. vsesoyuznogo simpoziuma po iskopaemym korallam, Tbilisi, 1978). – Akademiya Nauk SSSR, Otdelenie Geologii, Geofiziki i Geokhimii; 148–156, 200–201, pls. 17–18); Moskva (izdatel'stvo Nauka) (in Russian).

ILJINA, T.G. (1984): Istoricheskoe razvitie korallov. Podotryad Polycoeliina. [Historical development of corals, suborder Polycoeliina]. – Trudy Paleontologicheskogo Instituta (Moskva), Akademiya Nauk SSSR, 198: 1–184 (in Russian).

ILJINA, T.G. (1986): Mikro- i ul'trastruktura sept nekotorykh rugoz. [Micro- and ultrastructure of septa in some Rugosa]. – In: SOKOLOV, B.S. (ed.), Fanerozoyskie rify i korally SSSR (Trudy 5. vsesoyuznogo simpoziuma po korallam i rifam, Dushanbe, 1983). – Akademiya Nauk SSSR, Otdelenie Geologii, Geofiziki, Geokhimii i Gornykh Nauk; 81–83, 220–221, pl. 19; Moskva (izdatel'stvo Nauka) (in Russian).

International Code of Zoological Nomenclature. Fourth Edition. – I–XXIX, 1–306; London (Natural History Museum, International Commission on Zoological Nomenclature).

IVANOVSKIY, A.B. (1965): Drevneyshie rugozy. [The oldest Rugosa]. – Institut Geologii i Geofiziki, Akademiya Nauk SSSR, Sibirskoe Otdelenie; 1–152, 77 figs., 39 pls.; Moskva (Izdatel'stvo Nauka) (in Russian).

JANSEN, U., BECKER, G., PLODOWSKI, G., SCHINDLER, E., VOGEL, O. & WEDDIGE, K. (2004): Pragian and Emsian near Aouinet Torkoz (SW Dra Valley, Morocco). – In: EL HASSANI (ed.), Devonian neritic-pelagic correlation and events in the Dra Valley (Western Anti-Atlas, Morocco). Fieldtrip Guidebook, International Meeting on Stratigraphy, Rabat, March 1–10, 2004. – Documents de l'Institut Scientifique, Université Mohammed V, Agdal, Rabat, 19: 75–84.

JIANG SHUI-GEN (1982): Anthozoa. – In: The Palaeontological Atlas of Hunan. (ed.: Geological Bureau of Hunan; Ministry of Geology and Mineral Resources). – Geological Memoirs, series 2 (stratigraphy and palaeontology), number 1: 81–162, 820–842, pls. 46–112; Beijing (Geological Publishing House) (in Chinese).

JIN SHAN-YU (2005): Chapter 3. The fossil identification list and genera-species descriptions. – In: JIN Shan-yu, Shen An-jiang, Chen Zi-liao, Lu Jun-ming, Wei Min, Wang Yuan-qing & Xie Fei: Mixed Biostratigraphy of Devonian in Wenshan, Yunnan. – The 20th anniversary of the founding of Hangzhou Institute of Geology, CNPC (1984-2004); 22–138, 170–194, pls. 1–35; Beijing (Petroleum Industry Press) (in Chinese).

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.

KAYSER, E. (1883): Obercarbonische Fauna von Lo-ping. – In: RICHTHOFEN, F. v., China. Ergebnisse eigener Reisen und darauf gegründeter Studien. Band IV. Beiträge zur Paläontologie von China. – 160–208, pls. 19–29; Berlin (Verlag Dietrich Reimer).

KOCH, G.v. (1882): Mittheilungen über die Structur von *Pholidophyllum Loveni* E. und H. und *Cyathophyllum* sp.? aus Konieprus. – Palaeontographica (Cassel), 28(6): 213–223.

KOCH, G.v. (1896): Das Skelett der Steinkorallen. – Festschrift zum siebenzigsten Geburtstage von Carl GEGENBAUR am 21, August 1896, 2: 249–276; Leipzig (Wilhelm Engelmann).

KÖLLIKER, A.v. (1866): Icones Histiologicae oder Atlas der vergleichenden Gewebelehre. Zweite Abtheilung. Der feinere Bau der höheren Thiere. Erstes Heft. Die Bindesubstanz der Coelenteraten. – 87–181; Leipzig (Wilhelm Engelmann, dated 1865).

KOKER, E.M.J. (1924): Anthozoa uit het Perm van het eiland Timor. I. Zaphrentidae, Plerophyllidae, Cystiphyllidae, Amphiastraeidae. – Jaarboek van het Mijnwezen in Nederlandsch Oost-Indie ('s Gravenhage), 1922, Verhandelingen, 51: 1–50.

KONINCK, L.G. de (1872): Nouvelles Recherches sur les Animaux Fossiles du Terrain Carbonifère de la Belgique. Première Partie. – Mémoires de l'Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique (Bruxelles), 39: I–IV, 1–178.

KORN, D. & WEYER, D. (2003): High resolution stratigraphy of the Devonian–Carboniferous transitional beds in the Rhenish Mountains. – Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe, 6: 79–124.

KOSSOVAYA, O.L. (2007): Ecological aspects of upper Carboniferous – lower Permian "*Cyathaxonia* fauna" taxonomical diversity (the Urals). – Schriftenreihe der Erdwissenschaftlichen Kommissionen, Österreichische Akademie der Wissenschaften (Wien), 17. – In : HUBMANN, B. & PILLER, W. E. (eds.), Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera, Graz 2003): 383–405.

KULLMANN, J. (1965): Rugose Korallen der Cephalopodenfazies und ihre Verbreitung im Devon des südöstlichen Kantabrischen Gebirges (Nordspanien). – Akademie der Wissenschaften und der Literatur [in Mainz] (Wiesbaden), Abhandlungen der mathematisch-naturwissenschaftliche Klasse, 1965 (2): 33–168.

KUNTH, A. (1869): Beiträge zur Kenntniss fossiler Korallen. 1. Korallen des schlesischen Kohlenkalkes. – Zeitschrift der Deutschen Geologischen Gesellschaft (Berlin), 21(1): 183–220.

LAFUSTE, J.G. (1970): Lames ultra-minces à faces polies. Procédé et application à la microstructure des Madréporaires fossiles. – Comptes Rendus de l'Académie des Sciences, Paris, 270(2), série D: 679–681.

LANG, W.D. (1923): Trends in British Carboniferous Corals. – Proceedings of the Geologists' Association (London), 34(2): 120–136.

LANG, W.D. (1938): Some further considerations on trends in corals. – Proceedings of the Geologists' Association (London), 49(2): 148–159.

LANG, W.D., SMITH, S. & THOMAS, H.D. (1940): Index of Palaeozoic coral genera. – I–VII, 1–231; London [British Museum (Natural History)].

LAVRUSEVICH, A.I. (1968): Rugozy postludlovskikh otlozheniy doliny r. Zeravshan (tsentral'nyy Tadzhikistan). [Post-Ludlowian Rugosa from the valley of river Zeravshan (Central Tadzhikistan)]. – In: SOKOLOV, B.S. & IVANOVSKIY, A.B. (eds.), Biostratigrafiya pogranichnykh otlozheniy silura i devona [Biostratigraphy of Silurian-Devonian boundary beds]. – Institut Geologii i Geofiziki, Akademiya Nauk SSSR, Sibirskoe Otdelenie; 102–130, 1 tab., pls. 6–12; Moskva (Izdatel'stvo Nauka) (in Russian).

LIAO WEI-HUA & CAI TU-CI (1987): Sequence of Devonian rugose coral assemblages from northern Xinjiang. – Acta Palaeontologica Sinica (Beijing), 26(6): 689–707 (in Chinese; English summary).

LUDWIG, R. (1865–1866): Corallen aus paläolithischen Formationen. – Palaeontographica (Cassel), 14(4, 5, 6): 133–244, 249–252.

MILNE-EDWARDS, H. (1857–1860): Histoire naturelle des coralliaires ou polypes proprement dits. – vol. 1: I–XXXIV, 1–326, 1857; vol. 2: 1–633, 1857; vol. 3: 1–560, 1860; atlas, 1–11, 31 pls., 1857; Paris (Librairie encyclopédique RORET).

MILNE-EDWARDS, H. & HAIME, J. (1848): 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. (1850–1855): A Monograph of the British Fossil Corals. – The Palaeontographical Society (London), Monographs: I–LXXXV, 1–322 [Part 1, 1850: I–LXXXV, 1–72, pls. 1–11 (vol. 3–7); Part 2, 1851: 73–146, pls. 12-30 (vol. 5–12); Part 3, 1852: 147–210, pls. 31–46 (vol. 6–14); Part 4, 1853: 211–244, pls. 47–56 (vol. 7–20); Part 5, 1855: 245–322, pls. 57–72 (vol. 8–29, dated 1854)].

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.

MÜLLER-STOLL, H. (1936): Beiträge zur Anatomie der Belemnoidea. – Noca Acta Leopoldina (Halle), Neue Folge, 4(20): 157–226.

NICHOLSON, H.A. (1876): Notes on the Palaeozoic Corals of the State of Ohio. – The Annals and Magazine of Natural History (London), series 4, 18 (no. 104): 85–95.

NIERMANN, H.T. (1975): Polycoeliidae aus dem Oberperm auf Timor. – Münstersche Forschungen zur Geologie und Paläontologie, 37: 131–225.

OEKENTORP, K. (1972): Sekundärstrukturen bei paläozoischen Madreporaria. – Münstersche Forschungen zur Geologie und Paläontologie, 24: 35–109.

OEKENTORP, K. (1974a): Microstructures of Palaeozoic corals. – Trudy Instituta Geologii i Geofiziki, Sibirskoe Otdelenie (Novosibirsk), Akademiya Nauk SSSR, 201. – In: SOKOLOV, B.S. (ed.), Drevnie Cnidaria, tom 1. Trudy I. mezhdunarodnogo paleontologichekogo simpoziuma po izucheniyu iskopaemykh korallov, Novosibirsk 1971): 14–19, 268–269.

OEKENTORP, K. (1974b): Electron microscope studies on skeletal structures in Coelenterata and their systematic value. – Proceedings of the Second International Coral Reef Symposium, 2: 321–326; Brisbane (The Great Barrier Reef Committee).

OEKENTORP, K. (1980): Aragonit und Diagenese bei jungpaläozoischen Korallen. – Münstersche Forschungen zur Geologie und Paläontologie, 52: 119–239.

OEKENTORP, K. (1984): Aragonite and Diagenesis in Permian Corals. – Palaeontographica Americana (Ithaca/ New York), 54. – In: OLIVER, W.A. jr. et al. (eds.), Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983]: 282–293.

OEKENTORP, K. (1989): Diagenesis in corals: syntaxial cements as evidence for post-mortem skeletal thickenings. – Memoir of the Association of Australasian Palaeontologists (Brisbane), 8. – In: JELL, P.A. & PICKETT, J.W. (eds.), Fossil Cnidaria 5. Proceedings of the Fifth International Symposium on Fossil Cnidaria including Archaeocyatha and Spongiomorphs held in Brisbane, Queensland, Australia, 25–29 July 1988): 169–177.

OEKENTORP, K.A.W. (2001): Review on diagenetic microstructures in fossil corals, a controversial discussion. – Bulletin of the Tohoku University Museum, 1 (Proceedings of the 8th International Symposium on Fossil Cnidaria and Porifera September 12–16, 1999 Sendai, Japan): 193–209.

OGILVIE, M.M. (1897): Microscopic and Systematic Study of Madreporarian Types of Corals. – Philosophical Transactions of the Royal Society of London, B, 187 (1896): 83–345.

PFEIFFER, H. (1954): Der Bohlen bei Saalfeld/Thür. – Geologie (Berlin), Beiheft, 11: 1–105.

PLUSQUELLEC, Y., GOURVENNEC, R. & JAOUEN, P.-A. (2012): New data on *Angustiphyllum* ALTEVOGT, 1965, an automobile free-living rugose coral from the Eifelian of the Western Armorican Massif (France). – Geologica Belgica (Bruxelles), 15(4): 254–264.

PLUSQUELLEC, Y. & SEMENOFF-TIAN-CHANSKY, P. (1973): Révision de *Combophyllum osismorum* M.E. & H., 1850 (Tétracoralliaire dévonien). – Bulletin du Muséum National d'Histoire Naturelle, Paris, série 3, 100 (sciences de la terre, 20): 411–462 (dated 1972).

POČTA, P. (1902): Anthozoaires et Alcyonaires. – In : BARRANDE, J., Système Silurien du Centre de la Bohême. Partie I. Recherches Paléontologiques. VIII.2. – I–VIII, 1–347, pls. 20–118; Prague (éditée par le Musée Bohême).

PRATZ, E. (1882): Über die verwandtschaftlichen Beziehungen einiger Korallengattungen mit hauptsächlicher Berücksichtigung ihrer Septalstructur. – Palaeontographica (Cassel), 29(2): 81–124.

RODRÍGUEZ, S. (1989): Lamellar microstructure in Palaeozoic corals: origin and use in taxonomy. – Memoir of the Association of Australasian Palaeontologists, 8. – In: JELL, P.A. & PICKETT, J.W. (eds.), Fossil Cnidaria 5. Proceedings of the Fifth International Symposium on Fossil Cnidaria including Archaeocyatha and Spongiomorphs held in Brisbane, Queensland, Australia, 25–29 July 1988): 157–168.

ROMANO, S.L. & CAIRNS, S.D. (2000): Molecular phylogenetic hypotheses for the evolution of Scleractinian corals. – Bulletin of Marine Science (Miami), 67(3): 1043–1068.

RONIEWICZ, E. (1984): Microstructural evidence of the Distichophylliid affinity of the Caryophylliina (Scleractinia). – Palaeontographica Americana (Ithaca, New York), 54. – OLIVER, W.A. jr. et al. (eds.), Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983]: 515–518.

RONIEWICZ, E. (1989): Triassic scleractinian corals of the Zlambach Beds, Northern Calcareous Alps, Austria. – Denkschriften der Österreichischen Akademie der Wissenschaften (Wien), mathematisch-naturwissenschaftliche Klasse, 126: 1–152.

RONIEWICZ, E. & MORYCOWA, E. (1989): Triassic Scleractinia and the Triassic/Liassic boundary. – Memoir of the Association of Australian Palaeontologists (Brisbane), 8: 347–354.

RONIEWICZ, E. & MORYCOWA, E. (1993): Evolution of the Scleractinia in the light of microstructural data. – Courier Forschungsinstitut Senckenberg (Frankfurt/Main), 164: 233–240.

RÓŻKOWSKA, M. (1969): Famennian Tetracoralloid and Heterocoralloid fauna from the Holy Cross Mountains (Poland). – Acta Palaeontologica Polonica (Warszawa), 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.

SCHOUPPÉ, A. v. (1955): Neues zur Morphologie permischer Korallengenera. – Zeitschrift der Deutschen Geologischen Gesellschaft (Hannover), 105(3): 570–571.

SCHOUPPÉ, A. v. (1956): Neue Betrachtungen zur Skelettbildung der Pterocorallia. – Paläontologische Zeitschrift (Stuttgart), 30(3–4): 148–162.

SCHOUPPÉ, A. v. (1957a): Neues zur Skelettbildung der Pterocorallia. – Zeitschrift der Deutschen Geologischen Gesellschaft (Hannover), 1956, 108(2): 255–256.

SCHOUPPÉ, A. v. (1957b): Zwei Pterocorallia aus dem Perm von Portugiesisch Timor. – Neues Jahrbuch für Geologie und Paläontologie (Stuttgart), Abhandlungen, 104(3): 359–381.

SCHOUPPÉ, A. v. & STACUL, P. (1955): Die Genera *Verbeekiella* PENECKE, *Timorphyllum* GERTH, *Wannerophyllum* n. gen. und *Lophophyllidium* GRABAU aus dem Perm von Timor. – Palaeontographica (Stuttgart), Supplement-Band, 4. – In: WANNER, J. (ed.), Beiträge zur Geologie von Niederländisch-Indien (5) (3): 95–196.

SCHOUPPÉ, A. v. & STACUL, P. (1959a): Säulchenlose Pterocorallia aus dem Perm von Indonesisch-Timor (mit Ausnahme der Polycoeliidae). Eine morphogenetische und taxonomische Untersuchung. – Palaeontographica (Stuttgart), Supplement-Band, 4. – In: WANNER, J. (ed.), Beiträge zur Geologie von Niederländisch-Indien (5) (4): 197–359.

SCHOUPPÉ, A. v. & STACUL, P. (1959b): Die Fossula der Pterocorallia, ihre morphogenetische und taxonomische Bedeutung. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen (Stuttgart), 108(1): 21–46.

SCHOUPPÉ, A. v. & STACUL, P. (1961): Die Axialstruktur der Pterocorallia. – Neues Jahrbuch für Geologie und Paläontologie (Stuttgart), Abhandlungen, 112(3): 251–280.

SCHOUPPÉ, A. v. & STACUL, P. (1962): Das Stereoplasma der Pterocorallia, seine Genese und Struktur. – Neues Jahrbuch für Geologie und Paläontologie (Stuttgart), Abhandlungen, 114(1): 24–57.

SCHOUPPÉ, A. v. & STACUL, P. (1966): Morphogenese und Bau des Skelettes der Pterocorallia. – Palaeontographica (Stuttgart), Supplement-Band, 11: 1–186.

SCRUTTON, C.T. (1996): Ecophenotypic variation in the early Silurian rugose coral *Palaeocyclus porpita*. – Proceedings of the Yorkshire Geological Society (Bath), 51(1): 1–8.

SEMENOFF-TIAN-CHANSKY, P. (1984): Microstructure of *Siphonodendron* (Lithostrotionidae). – Palaeontographica Americana (Ithaca), 54. – In: OLIVER, W.A. jr. et al. (eds.), Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983: 489–500.

SEMENOFF-TIAN-CHANSKY, P. & NUDDS, J. R. (1979): Révision de quelques espèces de *Lithostrotion* des îles Britanniques décrites par Milne Edwards et Haime (Tétracoralliaires carbonifères). – Bulletin du Muséum National d'Histoire Naturelle (Paris), série 4, 1 (section C, 3): 245–283.

SIMPSON, G.B. (1900): Preliminary descriptions of new genera of Paleozoic Rugose corals. – Bulletin of the New York State Museum (Albany), 8(39): 199–222.

SMITH, S. (1928): The Carboniferous Coral *Nemistium edmondsi*, gen. et sp. n. – The Annals and Magazine of Natural History (London), series 10, 1(1): 112–120.

SOKOLOV, B.S. (1960): Permskie korally yugo-vostochnoy chasti Omolonskogo massiva (s obshchim obzorom plerofilloidnykh rugoz). [Permian corals from the south-eastern part of the Omolon massive, with a general review of plerophylloid Rugosa]. – Trudy, Vsesoyuznyy Neftyanyy Nauchno-Issledovatel'skiy Geologorazvedochnyy Institut (VNIGRI, Leningrad), 154 (Paleontologicheskiy Sbornik, 2): 38–77 (in Russian).

SORAUF, J.E. (1978): Original structure and composition of Permian rugose and Triassic scleractinian corals. – Palaeontology (London), 21(2): 321–339.

SORAUF, J.E. (1981): Biomineralization, structure and diagenesis of the Coelenterate skeleton. – Acta Palaeontologica Polonica (Warszawa), 25(3–4): 327–343 (dated 1980).

SORAUF, J.E. (1983): Primary biogenic structures and diagenetic history of *Timorphyllum wanneri* (Rugosa), Permian, Timor, Indonesia. – Memoir of the Association of Australasian Palaeontologists (Brisbane), 1: 275–288.

SORAUF, J.E. (1984): Upper Permian Corals from Timor and Diagenesis. – Palaeontographica Americana (Ithaca, New York), 54. – In: OLIVER, W.A. jr. et al. (eds.), Proceedings of the Fourth International Symposium on Fossil Cnidaria (and Archaeocyathids and Stromatoporoids) held in Washington, DC, U.S.A., August, 1983: 294–302.

SORAUF, J.E. & FREIWALD, A. (2002): Skeletal structure in the rugosan genus *Calophyllum* from Permian strata of Timor: Comparison with the living deep water coral *Lophelia pertusa*. – Coral Research Bulletin (Dresden), 7. – SCHRÖDER, S., LÖSER, H. & OEKENTORP, K. (eds.), Contributions to Coral Research. Commemorative volume to celebrate Dr. Dieter Weyer's 65th birthday): 191–207.

SORAUF, J.E. & JELL, J.S. (1977): Structure and incremental growth in the ahermatypic coral Desmophyllum cristagalli from the North Atlantic. – Palaeontology (London), 20(1): 1–19.

SOSHKINA, E.D. (1928): Nizhnepermskie (artinskie) korally zapadnogo sklona Severnogo Urala [Die unterpermischen Korallen vom westlichen Abhang des nördlichen Uralgebirges]. – Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, novaya seriya, 36, otdel geologicheskiy, 6 (3–4): 339–393.

SOSHKINA, E.D., DOBROLYUBOVA, T.A. & PORFIR'EV, G.S. (1941): Permskie Rugosa Evropeyskoy chasti SSSR. [The Permian Rugose Corals of the European Part of the USSR]. – Paleontologiya SSSR (Paleontologicheskiy Institut, Akademiya Nauk SSSR), 5 (3, 1): 19–304, 44 figs., 1 tab., 63 pls.; Moskva, Leningrad.

SOTO, F. (1982): Plerophyllidae y Pentaphyllidae (Coelenterata, Rugosa) del Devónico de la Cordillera Cantábrica (NO de España). – Trabajos de Geología, Universidad de Oviedo, 12: 49–61.

SOTO, F. & GARCIA-ALCALDE, J.L. (1976): La fauna silicificada del Devónico de Piedras Blancas. – Trabajos de Geología, Universidad de Oviedo, 8: 87–103.

STRUVE, A.O. (1898): Ein Beitrag zur Kenntniss des festen Gerüstes der Steinkorallen. – Zapiski Imperatorskago S.-Peterburgskago Mineralogicheskago Obshchestva [Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg], seriya 2, 35: 43–115.

SUTHERLAND, P.K. (1965): Henryhouse Rugose Corals. – Bulletin, Oklahoma Geological Survey (Norman), 109: 1–92.

SUTHERLAND, P.K. (1970): A redescription of the Silurian rugose coral *Syringaxon siluriensis* (McCoy). – Journal of Paleontology (Tulsa), 44(6): 1125–1128.

VAUGHAN, T.W. (1900): The Eocene and Lower Oligocene Coral Faunas of the United States, with Descriptions of a few doubtfully Cretaceous Species. – Monographs, United States Geological Survey (Washington), 39: 1–263.

VERON, J.E.N. & PICHON, M. (1982): Scleractinia of Eastern Australia. Part IV. Family Poritidae. – Australian Institute of Marine Science, Monograph Series (Canberra), 5: 1–159.

VOLZ, W. (1896): Die Korallenfauna der Trias. II. Die Korallen der Schichten von St. Cassian in Süd-Tirol. – Palaeontographica (Stuttgart), 43(1–2): 1–124.

WANG Hong-zhen [H.C.] (1950): A revision of the Zoantharia Rugosa in the light of their minute skeletal structures. – Philosophical Transactions of the Royal Society of London, series B, Biological Sciences, 234 (611): 175–246.

WEYER, D. (1971a): *Neaxon regulus* (RH. RICHTER, 1848), ein Leitfossil der mitteleuropäischen *Wocklumeria*-Stufe (Anthozoa, Rugosa; Oberdevon). – Geologie (Berlin), 20(3): 292–315.

WEYER, D. (1971b): *Famaxonia*, ein neues Rugosa-Genus aus der *Wocklumeria*-Stufe (Oberdevon) des Thüringischen Schiefergebirges. – Geologie (Berlin), 20(9): 1025–1033.

WEYER, D. (1972): Zur Morphologie der Rugosa (Pterocorallia). – Geologie (Berlin), 21(6): 710–737.

WEYER, D. (1973a): Einige Rugose Korallen aus der Erbslochgrauwacke (Unterdevon) des Unterharzes. – Zeitschrift für Geologische Wissenschaften (Berlin), Themenheft, 1: 45–65.

WEYER, D. (1973b): Über *Protozaphrentis* YÜ, 1957 (Anthozoa Rugosa, Mittelordoviz). – Paläontologische Abhandlungen (Berlin), Abteilung A, Paläozoologie, 4(4): 695–706.

WEYER , D. (1974): Zur Kenntnis von *Rhegmaphyllum* WEDEKIND, 1927 (Anthozoa, Rugosa; baltoskandisches Silur). – Zeitschrift für Geologische Wissenschaften (Berlin), 2(2): 157–183.

WEYER, D. (1975a): Korallen aus dem Obertournai der Insel Hiddensee. – Zeitschrift für Geologische Wissenschaften (Berlin), 3(7): 927–949.

WEYER , D. (1975b): Combophyllidae (Anthozoa, Rugosa) im Mitteldevon des Thüringischen Schiefergebirges. – Freiberger Forschungshefte, C 304: 7–31.

WEYER, D. (1978a): Zwei neue Rugosa-Genera aus dem marokkanischen und thüringischen Devon. – Jahrbuch für Geologie (Zentrales Geologisches Institut Berlin), [for] 1973/74, 9/10: 289–345.

WEYER, D. (1978b): Neue Sutherlandiniinae (Rugosa) aus dem skandinavischen Silur und aus dem thüringischen Devon. – Freiberger Forschungshefte, C 342: 91–116.

WEYER, D. (1978c): *Neaxon bartzschi*, eine neue Rugosa-Art aus der *Wocklumeria*-Stufe (Oberdevon) des Thüringischen Schiefergebirges. – Zeitschrift für Geologische Wissenschaften (Berlin), 6(4): 493–500.

WEYER, D. (1980a): Zwei *Ufimia*-Arten aus dem Erdbacher Kalk im Rheinischen Schiefergebirge (Anthozoa, Rugosa; Unterkarbon). – Abhandlungen und Berichte für Naturkunde und Vorgeschichte (Kulturhistorisches Museum Magdeburg), 12(2): 3–25 (dated 1979).

WEYER, D. (1980b: Die älteste Rugose Koralle Europas (*Primitophyllum* KALJO, 1956, Mittelordoviz). – Wissenschaftliche Beiträge der Martin-Luther-Universität Halle/Wittenberg, [for] 1978, 30 (P7, Kongress- und Tagungsberichte: Neue paläontologische und geologische Forschungsergebnisse hallenser Absolventen): 51–77 (dated 1978, issued 10.8.1980).

WEYER, D. (1981): Korallen der Devon/Karbon-Grenze aus hemipelagischer Cephalopoden-Fazies im mitteleuropäischen variszischen Gebirge – *Bathybalva* n. g., *Thuriantha* n. g. (Rugosa). – Freiberger Forschungshefte, C 363: 111–125.

WEYER, D. (1984a): *Neaxon cheilos* n.sp. aus dem Unterfamenne von Schleiz im Thüringer Schiefergebirge (Anthozoa, Rugosa; Oberdevon). – Abhandlungen und Berichte für Naturkunde und Vorgeschichte (Kulturhistorisches Museum Magdeburg), 12(5): 3–16, 77–83 (dated 1982, issued 23.2.1984).

WEYER, D. (1984b): Korallen im Paläozoikum von Thüringen. – Hallesches Jahrbuch für Geowissenschaften (Gotha), 9: 5–33.

WEYER, D. (1985): Zur Kenntnis eurasiatisch-nordafrikanischer Emsium/Eiflium-Hapsiphyllidae (Anthozoa, Rugosa; Devon). – Abhandlungen und Berichte für Naturkunde und Vorgeschichte (Kulturhistorisches Museum Magdeburg), [for 1984], 12(6): 15–35.

WEYER, D. (1991): *Pseudopetraia* SOSHKINA 1951 (Anthozoa, Rugosa) aus dem Unterdevon des Thüringischen Schiefergebirges. – Abhandlungen und Berichte für Naturkunde und Vorgeschichte (Kulturhistorisches Museum Magdeburg), 15: 9–24.

WEYER, D. (1993): Korallen aus dem Obertournai und Untervisé der Inseln Hiddensee und Rügen. – Abhandlungen und Berichte für Naturkunde (Museum für Naturkunde Magdeburg), 16: 31–69.

WEYER, D. (1994): Korallen im Untertournai-Profil von Drewer (Rheinisches Schiefergebirge). – Geologie und Paläontologie in Westfalen (Münster), 29: 177–221.

WEYER, D. (1995): Heterocorallia aus Famenne-Cephalopodenkalken im Rheinischen Schiefergebirge und Tafilalt. – Abhandlungen und Berichte für Naturkunde (Museum für Naturkunde Magdeburg), 18: 103–135.

WEYER, D. (1996): *Nichlavalla sytovae* n. g. n. sp. aus dem Lochkovian von Podolien (Anthozoa, Rugosa; Unterdevon, Ukraine). – Abhandlungen und Berichte für Naturkunde (Museum für Naturkunde Magdeburg), [for 1995], 19: 83–103.

WEYER, D. (1997): Hyposepta and diplosepta in the septal apparatus of Rugosa. – Boletín de la Real Sociedad Española de Historia Natural (Madrid), Sección Geológica, 91 (1–4). – In: PEREJÓN, A. & COMAS-RENGIFO, M.J. (eds.), Proceedings of the VII International Symposium on Fossil Cnidaria and Porifera held in Madrid, Spain, 1995): 37–52.

WEYER, D. (2002): *Guerichiphyllum* RÓZKOWSKA 1969 (Anthozoa, Rugosa) aus dem Ober-Famennian (*Wocklumeria*-Stufe) von Saalfeld in Thüringen. – Abhandlungen und Berichte für Naturkunde, Museum für Naturkunde Magdeburg, 25: 15–24.

WEYER, D. (2005): Über *Tetralasma* SCHINDEWOLF 1942 (Anthozoa, Rugosa; Unterkarbon). – Abhandlungen und Berichte, Museum für Naturkunde (Magdeburg), 28: 23–35.

WEYER, D. (2008): Revision des LUDWIG/KUNTH-Gesetzes zur Septeninsertion der Supraordo Rugosa (Anthozoa, Ordoviz—Perm). – Abhandlungen und Berichte für Naturkunde (Museum für Naturkunde Magdeburg), 30: 85–145 (dated 2007, issued 22.8.2008).

YOH SEN-SHING, JIN SHAN-YU, ZHEN YONG-YI & XIE FEI (1984): New discovery of Lower Devonian Heterocorallia corals from south-eastern Yunnan. – Scientific Achievements of Professor Yoh Senshing, Symposium of the Department of Geology, Beijing University: 1–8, 263, pl. 1; Beijing (Geological Publishing House) (in Chinese; English summary).

ZHAO JIA-MING (1976): Late Permian rugose corals from Anshun, Luzhi and Qinglong, Guizhou province. – Acta Palaeontologica Sinica (Beijing), 15(2): 213–223 (in Chinese, English summary).

ZHU ZHENG-GANG, REN RUN-SHENG, QI DUN-LUN, WU WANG-SHI, YAN YOU-YING, YU CHANG-MIN, YU XUE-GUANG, ZHAO JIA-MING, CHEN HUA-CHENG, CHEN M.-J. & LIAO WEI-HUA (1982): Anthozoa. – In: Paleontological Atlas of East China. 2. Volume of Late Paleozoic. (ed.: Nanjing Institute of Geology and Mineral Resources, Ministry of Geology). – 108–179, 445–457, pls. 31–70; Beijing (Geological Publishing House) (in Chinese).

psf – Paläontologie, Stratigraphie, Fazies

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