

## Review of some Frasnian ahermatypic coral localities from Germany and description of a new genus *Spinaxon* (Anthozoa, Rugosa, Upper Devonian)

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**ABSTRACT.** One of the greatest gaps in the present worldwide knowledge of Rugosa history are the unstudied ahermatypic coral faunas of Frasnian (and Upper Givetian) times, though they exist in many places. Most occurrences in Germany are briefly reviewed (Variscan Rhenish, Harz, Thuringian and Franconian Mountains; Baltoscandian shelf deposits in deep boreholes on the Baltic Sea island of Rügen). Intensive collecting in Thuringia presented rich Upper Frasnian samples from two localities (former Geipel quarry in the town of Schleiz, Vogelsberg-quarry near the village Tegau), dominated by *Metriophyllum* Milne-Edwards & Haime, 1850, *Neaxon* Kullmann, 1965, and the newly established genus *Spinaxon* (suborder Cyathaxoniina, family Petriidae), with the monotypic type species *Spinaxon potyi* sp. nov. Cephalopod limestones yielded >100 specimens of this taxon; one specimen was found in the Montagne Noire (Frasnian Famennian boundary stratotype section Coumiac). The taxon descends from *Neaxon* Kullmann, 1965 or its nearest relative *Petraia* Münster, 1839; it is characterized by unique hypertrophic long trabecular spines on the margins of major septa within an aulos of circulotheca type.

**KEYWORDS:** Frasnian, Kellwasser, ahermatypic Rugosa, Thuringia, Montagne Noire

### 1. Introduction

The Palaeozoic superorder Rugosa passed through several crises before the final extinction at the Permian–Triassic boundary. The most important one, the global Upper Kellwasser Event at the Frasnian–Famennian boundary, led to the disappearance of all coral reefs; they reappeared during top-Famennian times (Strunian). For a long period, the coral world of the Famennian (both photic and aphotic zones) was a *terra incognita* – but this changed surprisingly after the monograph of Polish ahermatypic Famennian Rugosa (Rózkowska, 1969), and with the discovery of similar faunas mainly in Germany and Morocco, and also in northern China (Liao & Cai, 1987; Cai, 1988; Wu & Liao, 1988; Guo 1990). Knowledge about Famennian shallow water Rugosa increased more slowly: especially through Sorauf (1992: unique first upper Famennian, though pre-Strunian Rugosa fauna from North America) and Berkowski (2002: first upper Famennian, also pre-Strunian survivors of Frasnian Phillipsastreidae in Poland). Unfortunately, up to now there still are no certain Rugosa occurrences from the basal Famennian (Lower, Middle, and Upper *Palmatolepis triangularis* Zones, perhaps also Lower *Palmatolepis crepida* Zone). The only one Rugosa, which I could collect from the Middle *Palmatolepis triangularis* Zone, together with *Nephranops incisus* (Roemer, 1866), was an undeterminable ampleximorph taxon from Rübeland in the German Harz Mts.

At present, the Upper Givetian and the Frasnian ahermatypic Rugosa are the main worldwide information gap (in contrast to the broad knowledge about shallow-water corals of the same time span). Thus, Sorauf & Pedder (1986, p. 1267) could speculate about a possible late origin of the basinal coral faunas in the Famennian – in reality they existed since the Silurian (rare in Wenlock, more often in Ludlow beds), but the majority remained unstudied and often even uncollected. Nowadays, nearly everywhere there are too few coral palaeontologists; so we must confess that e.g. the outstanding older monograph of Počta (1902) dealing with sometimes richer ahermatypic Ludlowian–Eifelian Rugosa from the famous Barrande collections in Bohemia, is still unrevised and nobody can interpret the many species using current actual taxonomy.

There prevail only scattered descriptions of Frasnian ahermatypic Rugosa, mostly isolated taxa in older literature, which often are in strong need of morphological revisions. Some of them were on the level of its time, e.g. *Nicholsoniella baschkirica* Soshkina, 1952 from middle Frasnian of the Southern Ural Mts. (Soshkina (1952, 1960), partly revised in Weyer (2000)). Others as some upper Frasnian species from the Kuznez Basin did not consider the currently necessary, more intensively investigated ontogenetic stages: *Nicholsoniella conica* Bul’vanker, 1958, *Nicholsoniella tomiensis* Bul’vanker 1958, *Nalivkinella brevisseptata* Ivaniya, 1965. Several “revisions” of *Metriophyllum* Milne-Edwards & Haime, 1850 (Smith, 1945; Holwill, 1964; Weyer, 1970 – accepted in Hill (1981), but

criticised in Weyer (1991)) used incorrect “topotypes”: there exist two different unrelated genera with metriophyllid carinae in the Lower Frasnian of Ferques (Boulonnais, NW France). A thorough monograph of the corals from the Independence Shale of Iowa was published by Stainbrook (1946). Hill & Jell (1971, western Australian Canning Basin) includes a modern study of several ahermatypic taxa. The contribution of Chinese authors to describe these Frasnian corals should be reviewed in that country.

### 2. Ahermatypic Frasnian Rugosa in Germany

The preliminary and subjective review of these mostly unknown and rare faunas is based on the few published studies and on available materials of some personal or museum collections. Undetermined and old-fashioned records in faunal lists are only partially mentioned; nevertheless they indicate a far greater distribution of such generally neglected corals.

#### 2.1. Rhenish Mountains

This outstanding German Devonian area contains many Frasnian ahermatypic Rugosa, which remain mostly unexplored up to present times. Of course, there exist several mere records of such corals or old-fashioned determination in faunal lists, e.g. Schmidt (1921, p. 268: *Amplexus* sp., from Belecke, Belecke Anticline), Schindler (1990, p. 35, fig. 8, also Feist & Schindler 1994, p. 198, fig. 2, Schmidt quarry S of Bad Wildungen, Kellerwald region), Schindler (1990, p. 40, fig. 11, Benner quarry near Bicken, Dill Syncline). Real palaeontological descriptions are rare exceptions and have never been revised: Ludwig (1865-1866), or Paeckelmann (1922: *Amplexus* sp. aff. *helminthoides* Frech, 1885, *Metriophyllum?* *irregulare* n. sp.). My access to this region started at first in 1990 after the reunification of the two German states, but was mainly concerned with Famennian and Lower Carboniferous strata, without intensive collecting in Frasnian beds. Some most promising localities can be mentioned.

*Martenberg near Adorf (now Diemelsee), east Sauerland region*

A first monographic study of the Middle Givetian–Lower Famennian sequence at this famous locality, a remnant of an ancient iron ore open-pit mine, was by Holzapfel (1882, p. 259) – aside from the dominating ammonoids, he mentioned in a faunal list “*Petraja radiata* Münster” and several “*Cyathophyllum*- and *Amplexus*-like” coral fragments. Such old-fashioned determinations can not be interpreted in modern taxonomy without the original specimens, which surely are lost.

Rugosa seem to be less rare, but nobody ever had assembled systematic collections. An excursion in 1991, guided by Jürgen Kullmann and Dieter Korn, was allowed to take only a few loose pebbles (due to the protected status of the outcrop); they yielded four still undetermined Rugosa, approximately from the lower Frasnian level of beds 14-16 (Ziegler & Sandberg, 1990, p. 26, fig. 3). Because of the difficult section situation (Kullmann & Ziegler,

1970; House & Ziegler, 1977) – extremely condensed, some hiatus – very precisely bed by bed sampling would be necessary, controlled by accompanying ammonoids and conodonts, and with permission of the natural reservation authorities.

In 2003, Ralph Thomas Becker presented me one *Rugosa* from the middle Givetian of Martenberg: it is identical with *Laccophyllum* sp. of Weyer & Zagora (1990, p. 26, fig. 2.1-6) from the same time level (“*Stringocephalus* Limestone” in Greifenstein facies, middle *Polygnathus varcus* Zone) of the classical Givetian locality Büchenberg N of Elbingerode in the Harz Mountains. This species is now determined as *Hamarophyllum* aff. *belkai* Berkowski, 2004 (Lower Emsian, Tafilalt, Morocco) – the age difference suggests caution over the true specific identity.

#### *Mount Beul near Eisborn, Sauerland region*

Small excavations near the top of the hill present the anoxic Upper Kellwasser Limestone, and below it 0.50 m cephalopod limestone (3 beds) – Lower *Palmatolepis linguiformis* Zone. The locality was mentioned in Wedekind (1913, p. 32, dealing with the ammonoid fauna), Becker (1993, p. 55), and Feist & Schindler (1994, p. 200, with illustrations of the trilobite fauna). During an excursion in 1992 (with Raimund Feist and Dieter Korn), I collected ten *Rugosa* (nine *Metriophyllum* sp., one *Neaxon* sp.).

#### *Sessacker trenches near Oberscheld, Dill Syncline*

Frasnian trilobites and ammonoid faunas are well known since Richter & Richter (1926, p. 279), Matern (1931), and the repeated famous Senckenbergian excavations. In 1995, Raimund Feist donated a *Rugosa* coral (collected in 1993) from trench no. VI, bed 21: a 12 cm-thick limestone just below the Upper Kellwasser Limestone, dated as Lower *Palmatolepis linguiformis* Zone. The specimen is determined as *Neaxon* sp. A locality reference was given by Feist & Schindler (1994, p. 199 fig. 3, also mentioning the presence of rugose corals). Surely, the extensive collections in the Senckenberg Museum at Frankfurt Main will reveal further unstudied coral materials

#### *Ancient iron ore mines around Oberscheld, Dill Syncline*

Ludwig (1865-1866) had described several corals from this region; all the outcrops are gone. The fossils were collected mainly by miners and now are found in many museum institutions: to name the Sandbergers collection in Wiesbaden, or the Rhenish Devonian collection of the former Prussian Geological Survey in Berlin (transferred in 1950 to the Humboldt University Berlin and stored at the Museum of Natural History). For a long period, the greater part of such faunas (with famous ammonoids) was accepted to be of lower Upper Devonian (Frasnian) age. Today, after radical stratigraphic changes and the fixation of new international time boundaries by means of stratotypes, the range of the iron ore horizon is Middle Givetian (*Maenioceras terebratum* Zone), Upper Givetian (“*Pharciceras* Zones”, the classical German “toIa” of Wedekind 1913, 1918), and lower Frasnian (up to the *Koenerites lamellosus* Zone).

The majority of the coral taxa (*Rugosa*, *Tabulata*) will be of Upper Givetian age, but a precise revision is extremely difficult and demands ammonoid control, which sometimes might be possible with such old collections when bearing precise locality data (e.g. “mine Königszug, 60 m depth level, collection Lotz 1901-1902”, or “mine Königszug, Westfeld, collection Ahlburg”). These are Ludwig’s coral taxa: *Rugosa*: *Amplexus umbilicatus* Ludwig, 1865; *Anorygmaphyllum obtusum* Ludwig, 1865; *Hexorygmaphyllum radiatum* Ludwig, 1866; *Liocyathus loculatus* Ludwig, 1866; *Ptychocyathus excelsus* Ludwig, 1866; *Taeniocyathus trochiformis* Ludwig, 1865. *Tabulata*: *Liodendrocyathus tubaeformis* Ludwig, 1866 [= *Cladochonus*]; *Liocalamocyathus cancellatus* Ludwig, 1866.

The taxonomy of all these species has never been revised. Only Schindewolf (1930; p. 124, fig. 15; 1931, p. 631-633; 1932, p. 471, fig. 1) used for a certain time the genus name *Ptychocyathus* Ludwig, 1866 (as a senior synonym of *Alleynia* Počta, 1902), and intended to prepare a revision of *Taeniocyathus* Ludwig, 1866, which remained uncompleted and unpublished. Thus, in reality the coral faunas of the long-lasting iron horizon are unknown according to the standards of our time, and are difficult to re-describe, as all their localities have disappeared.

I know a few specimens in old Berlin collections, bearing the generic and specific names of Ludwig on their labels and suitable as topotypes.

Momentary, the publication of Ludwig (1865-1866) was declared to be invalid and put on the index of publications unavailable for zoological nomenclature (Opinion 946 ICZN, 1971). This was an unjustified and unacceptable act similar to the now formalized Devonian ammonoid case of Sobolev (1914a, 1914b) – both authors had proposed formulae instead of normal generic names. Therefore it would have been appropriate to suppress all the new genera of Ludwig, but not his species. By Opinion 2337 (2014), the International Commission of Zoological Nomenclature revised their earlier incorrect decision and re-established the validity of Sobolev’s specific names: the same correction should be done for Ludwig (1865-1866).

## **2.2. Harz Mountains**

Not one ahermatypic *Rugosa* from the Frasnian cephalopod facies was available to me. Solitary corals were mentioned in faunal lists of the Adorf-Limestone (Frasnian) of the western Harz Mts. – without any precise locality (Beushausen, 1900, p. 165, re-cited in Schriell, 1954, p. 95), famous type locality Kellwasser valley near Altenau (“Upper *Palmatolepis rhenana* Zone” above the Lower Kellwasser Event, Schindler, 1990, p. 50, fig. 19). These records could mean undeterminable fragments or unstudied materials.

An exceptional record of *Metriophyllum* sp. is one sample from the Winterberg quarry in the famous Iberg reef near Bad Grund (1990 donated by Eberhard Gischler, then Göttingen – his conodont sample 70 – Gischler, 1992, p. 140, fig. 40). It is a foreereef limestone with reefal debris (big colony of the *Tabulata* coral *Alveolites*); this S-SE part of the quarry represents the Upper Frasnian (Upper *Palmatolepis rhenana* Zone) luff position of the atoll (Gischler, 1992, p. 26). There several limestone blocks contain a curious faunal mixture of destroyed reef corals (photic zone), benthic brachiopods of another community in somewhat deeper environment (probably with the ahermatypic *Rugosa*), and goniatites drifted perhaps as dead shells by prevailing SE trade-wind.

## **2.3. Western Thuringian Mountains (SE flank of Schwarzburg Anticline)**

In this part of the Thuringian Slate Mountains (with prevailing Frasnian cypridinic shale facies), really rare ahermatypic *Rugosa* were collected over a long period by local geologists and amateurs: near the town Steinach by Max Volk (1900-1969) in 1921-1938, near the town Saalfeld by Heinz Pfeiffer (1921-1994) in 1946-1955, Wilhelm Reuter (1925-1988) in 1970-1985, and Konrad Bartzsch in 1954-1965.

#### *Steinach area*

The somewhat richer materials around Steinach had been found in the period of active whetstone quarries, the last one of which was abandoned in 1966; nowadays all these once famous outcrops are gone (overgrown by vegetation). Weissermel (1939) described the collection; the greater part of his results is included in the publication of Volk (1939, pp. 265-266), which is indispensable for an understanding of the stratigraphical interpretation.

The detailed ages of the Upper Devonian coral faunas in Weissermel (1939) are doubtful for everybody not acquainted with the local stratigraphy. Weissermel used the abbreviations “tob, toc, toa” written on the labels of the Max Volk collection, and explained in Volk (1939, p. 151). These terms are the official mapping units, used for the Upper Devonian of Thuringia in the special geological maps 1:25 000 of the former Prussian Geological Survey (Preussische Geologische Landesanstalt) in Berlin, and introduced by Deubel (1929, pp. 69, 72, 76). Their modern terminology follows Bartzsch et al. (1999, pp. 167-172, 2008, p. 61):

tob = c. 40-50 m Braunwacken and Braunschiefer = Weinberg Member of Hirtenrangen Formation (middle-upper Frasnian).

toc = c. 60-75 m Tonschiefer (Cypridinen-Schiefer) = Lerchenberg Member of Hirtenrangen Formation (upper Frasnian) + Plattenbruch Member of Bohlen Formation (lower Famennian, Nehden substage, *Cheiloceras* genozone). Volk (1939) did not

mention the Upper Kellwasser Event as dividing horizon between these two members, but he separated them as toIδ and toII according to his biozones using entomozoid ostracods (following and improving Matern (1929)).

toa = großknotige Kalkknotenschiefer = Mühlfelsen Member and Breternitz Member of Gleitsch Formation (upper Famennian, starting above the global *Annulata* Event).

Frasnian Rugosa in Weissermel (1939) are the following “taxa”, cited according to his determinations (an \*asterisk marks “taxa” said to occur in the lower Famennian, too; one specimen marked by “?” lacks any stratigraphical and locality data and could be either Frasnian or lower Famennian):

\* p. 354, plate 14/15-17 *Syringaxon (Alleynia) thuringiacus* Weissermel, 1939

? p.355 *Syringaxon (Barrandeophyllum)* sp.

p. 359, plate 14/3 *Zaphrentis* sp.

\* p. 360, plate 14/4-8 *Zaphrentis curvatissima* Weissermel, 1939

\* p. 361, plate 14/9-10 *Metriophyllum volki* Weissermel, 1939

p. 362, plate 14/13-14 *Amplexus liliiformis* Weissermel, 1939.

Note: Weissermel (1943, p. 11) corrected the determination of plate 14/8, being *Zaphrentis curvatissima*, not *Metriophyllum volki*. There (p. 6, pl. 1/3,4), he also identified – erroneously – a Frasnian Rugosa from a 19<sup>th</sup> century locality Kirschkau NE of Schleiz (Planschwitz Beds) with his originally lower Famennian *Lindstroemia? cornuhirci* Weissermel, 1939.

All these taxa seem to be useless *nomina dubia* – due to the bad preservation (decalcified casts), insufficient morphological analysis and illustrations, no designation of holotypes. Besides, the *Syringaxon (Alleynia) thuringiacus* is a junior synonym of *Neaxon pauciradiatus* (Ludwig, 1865), a lower Famennian (*Cheiloceras* Genozone) species, found in the Plattenbruch Member (Bohlen Formation) of the Bohlen section near Saalfeld, well described by its author as *Amplexus* (based on material preserved mainly as casts).

Unfortunately, all the figured specimens, which in the cases of the four proposed new species of Weissermel (1939) could become possible lectotypes, are most probably lost. The loaned collection had been sent back to Max Volk by Waldemar Weissermel in about 1938-1940; then Max Volk had deposited the material in the Geological Institute of the University in Erlangen (as intended, Volk, 1939, p. 151). After the war, this institution more and more neglected its ancient collections – a deplorable actual situation in many German universities. Some small parts of the Max Volk collections were transferred to

the whetstone museum (Schiefer-Museum) in his hometown Steinach, but there I could find only one badly preserved coral specimen labelled in the characteristic handwriting of Waldemar Weissermel (and not illustrated in his 1939 publication). In 2015, Dr. Michael Heinze (curator of the palaeontological collections, Geozentrum, Universität Erlangen) kindly informed me that they do not possess the Weissermel 1939 coral collection. Dr. Manfred Bayer (same institution) told me that some older collections were in about 2005 transferred to Nürnberg (Naturhistorische Gesellschaft); there, Dr. Gottfried Hofbauer, who once had made an inventory of that transaction, could only ascertain the absence of the Weissermel 1939 corals. Obviously, inadequate care and curatorship in Erlangen is responsible for the almost certain loss of the unique and nowadays unrecoverable Rugosa fauna.

Very few specimens from the Frasnian Max Volk collection remained in Berlin with Waldemar Weissermel. Mostly, at that time these were indeterminate corals (e.g. small size, calcareous preservation, with no chance for preparation of thin sections). After his death (1943), they were stored together with many other corals (mainly Devonian of Thuringia and the Bosphorus) in a special cupboard as his left legacy. As responsible custodian I had to rearrange these faunas in 1966 according to the existing publications of Weissermel (1935-1943); this resulted in three revisions (Weyer, 1977, 1981, 1984b) of selected material.

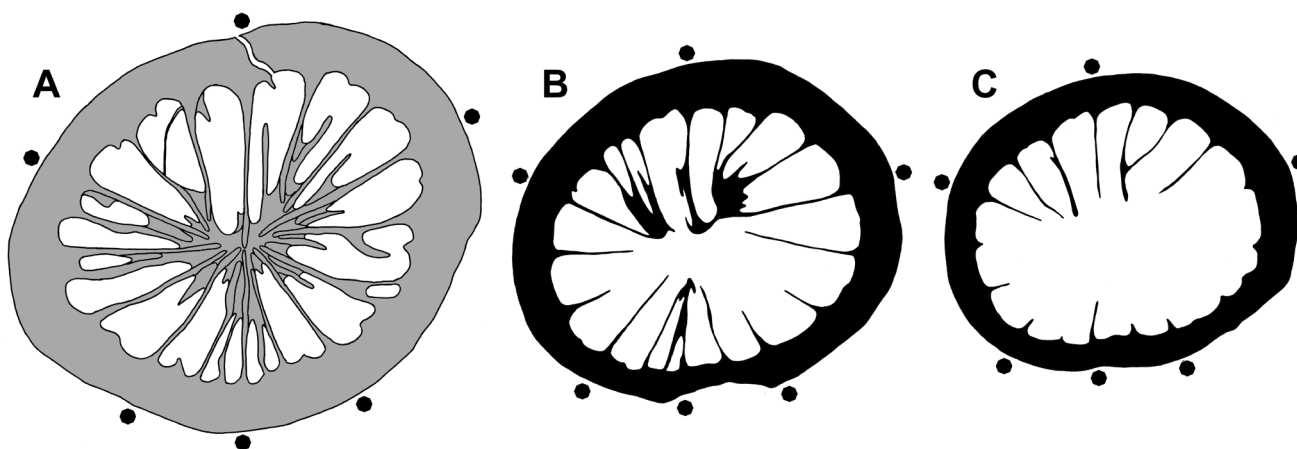
Later preparation of three such specimens allowed a determination as *Metriophyllum* sp. (Fig. 1), of course not identical with the doubtful “*Metriophyllum volki* Weissermel, 1939” of unknown generic position. The two specimens unfigured here are:

BGR.Berlin-X6604 – Mount Hirtenrangen NE Steinach (section 38 of Volk, 1939, p. 157), Upper Frasnian (Upper *Palmatolepis rhenana* Zone, *Rabienella reichi* Zone of entomozoid ostracods), lower Lerchenberg Member (Beds 76-84 = “Pferd”, Volk, 1939, p. 185), collection Max Volk 1921-1938.

BGR.Berlin-X6603 – Mount Hofberg near village Hasenthal NE Steinach (section 51 of Volk, 1939, p. 158), middle Frasnian, Weinberg Member of Hirtenrangen Formation, collection Max Volk 1921-1938; determined by Weissermel (and mentioned by Volk, 1939, p. 220) as *Zaphrentis* sp. aff. *curvatissima*.

#### Saalfeld area

The scarce available unstudied materials comprise about 10 ahermatypic Rugosa from the famous Bohlen section NNW of Saalfeld-Obernitz (Pfeiffer, 1954, annexes 1, 2); Bartzsch & Weyer, 2012, fig. 1). They were found in the Hirtenrangen Formation: both in the middle Frasnian Weinberg Member (Braunwacke, Braunschiefer), and in the Upper Frasnian Lerchenberg Member (Wetzschiefer). Nearly all represent a new small species of *Metriophyllum* Milne-Edwards & Haime, 1850.



**Figure 1.** *Metriophyllum* sp., abandoned whetstone quarry at mount Lerchenberg, southern Steinach, Upper Frasnian (Upper *Palmatolepis rhenana* Zone), basal Lerchenberg Member (of Hirtenrangen Formation), bed 29 in section 20 of Volk (1939, pp. 175, 187), 3.80 m above the Lower Kellwasser Event (= bed 3+4 in Volk, 1939, p. 189); collection Max Volk 1921-1938, no. BGR,Berlin-X6602. A. cross section at calicular base, x10 (few subtabular interseptal lumina at the antiseptum and its catasepta); B, C. cross sections in the lower calice, x7 and x6 (with typical *Metriophyllum* features: long cardinal septum, well developed antiseptal triade, other minor septa extremely short, septal microstructure trabicular). See Table 1 for septal formulae.

#### 2.4. Eastern Thuringian Mountains (NW flank of Berga Anticline)

Middle?–Upper Frasnian cephalopod limestones of this region sometimes yield comparatively rich, though rarely collected and mainly unstudied ahermatypic Rugosa. Mostly, they can be found during the active period of quarries. The small solitary corals are enclosed in hard limestone, generally without a chance to isolate them; the best collecting method is to break the rock perpendicular to the bedding plane, to look for suitable cross sections, and to saw them out of the stone in an accurately oriented manner.

Two ancient quarries, abandoned long ago, were visited without measurements of the section: former Braunsberg quarry ESE of Tegau (with strong tectonical dislocations, active mainly in the 19<sup>th</sup> century), and Kapfenberg quarry just N of Pahren, active 1897–1976, both mentioned in Müller (1956, p. 16). Loose limestone blocks of the Upper Frasnian (around the two Kellwasser Limestones, with locally famous homocentrite) yielded a few Rugosa, with one specimen of *Spinaxon potyi* from the Braunsberg quarry.

##### Former Geipel quarry in Schleiz

The first record was by Zimmermann (1915, p. 41 – small solitary corals, *Cyathophyllum* sp.). By chance, some of his few sampled Rugosa are preserved; they were deposited in the Devonian collections of the Thuringia province in the former Prussian Geological Survey, destroyed during the war in 1944. However, Otto Heinrich Schindewolf (member of the staff since 1929, later head of the collection department in this institution) had selected these specimens for his own studies, preserving them in his coral cupboards, where they survived. This also included some Upper Frasnian Rugosa from the immediately neighbouring former, now vanished Handmann quarry (mentioned in Müller, 1956, p. 11), obtained by Zimmermann in 1912 from the quarry owner Mr Handmann (a well known manufacturer in the town of Schleiz, just as Mr Geipel). About 1919, Schindewolf (1921, p. 172) visited the Geipel quarry and published a faunal list of Upper Frasnian ammonoids; the Rugosa also collected remained unpublished, but some first cross sections were prepared – they represent *Metriophyllum* sp. (Museum für Naturkunde, Berlin).

My own rich collection of 1995 (>100 Rugosa) comes from the 27 cm-thick last limestone bed just below the Upper Kellwasser Event – high Upper *Palmatolepis rhenana* Zone and lower *Palmatolepis linguiformis* Zone. A preliminary note (Weyer et al., 2003, p. 74, fig. 2) gives a first impression of the unexpectedly diverse coral fauna, dominated by *Metriophyllum*, accompanied by *Neaxon*, *Petraia* (*sensu* Weyer, 2000), *Metriaxon*, ampleximorph genera, and including also two specimens of the here described new taxon *Spinaxon potyi*.

##### Former Kahlleite quarry 1 km SW of Rödersdorf (NNE of Schleiz)

The locality offered an excellent Upper Devonian section (middle upper Frasnian – middle upper Tournaisian) during the quarrying period (Bartsch et al., 1993, pp. 12–13, 2001, p. 104, 2008, figs 9–10; Gereke, 2004). This was finished in 2013; now the good outcrop condition has disappeared. In 1984–1985, I could collect eight loose limestone blocks containing 27 Rugosa corals; their age was always controlled by accompanying conodonts. They come from the cephalopod limestone sequence below the Lower Kellwasser Event, immediately below the “Ostracode Limestone” (= Usseln-Limestone of Gereke (2004), the starting point of his detailed measured section figure 5) – Lower *Palmatolepis rhenana* Zone and Upper *Palmatolepis rhenana* Zone. Among the Rugosa fauna (with *Neaxon* and *Metriophyllum*), there are 2 specimens of *Spinaxon potyi*.

##### Vogelsberg quarry 1 km NNE of Göschitz (NNE of Schleiz)

For the moment, this outcrop (active since 1907 – Fig. 2) seems to be the best coral locality for Upper Frasnian ahermatypic Rugosa throughout the world. In certain beds of the cephalopod limestones, about 50 Rugosa will be found upon 1 goniatite – *Beloceras sagittarium* (Sandberger & Sandberger, 1851) and Gephuroceratidae. Perhaps, worldwide there might exist even better and richer coral occurrences, but up to now they remain uncollected and unstudied.



**Figure 2.** Vogelsberg quarry NNE of Göschitz before 1972, with remarkable fold in Frasnian-Famennian cephalopod limestones taken as marble blocks (destroyed in 1972–1973 by first use of dynamite to start a new technology for agglomerate marble, in relicts still preserved in Fig. 3).

In the years 1980–1983, also an excellent, still undescribed lower middle Famennian Rugosa fauna was collected at this locality (Weyer, 1984c, p. 19; 2004, p. 205) – from upper Nehdenian beds (Lower *Palmatolepis marginifera* Zone) with *Paratornoceras lentiforme* (Sandberger, 1857) and *Acrimeroceras* sp., and from the lower Hembergian (Upper *Palmatolepis marginifera* Zone) with *Pseudoclymenia pseudogoniatites* (Sandberger, 1853) and *Cycloclymenia planorbiformis* (Münster, 1832). *Thecaxon horni* Weyer, 2004, *Kozłowskinia flos* Różkowska, 1969, *Laccophyllum thuringicum* Weyer, 2004, and some new taxa occur there. These beds are now quarried away.

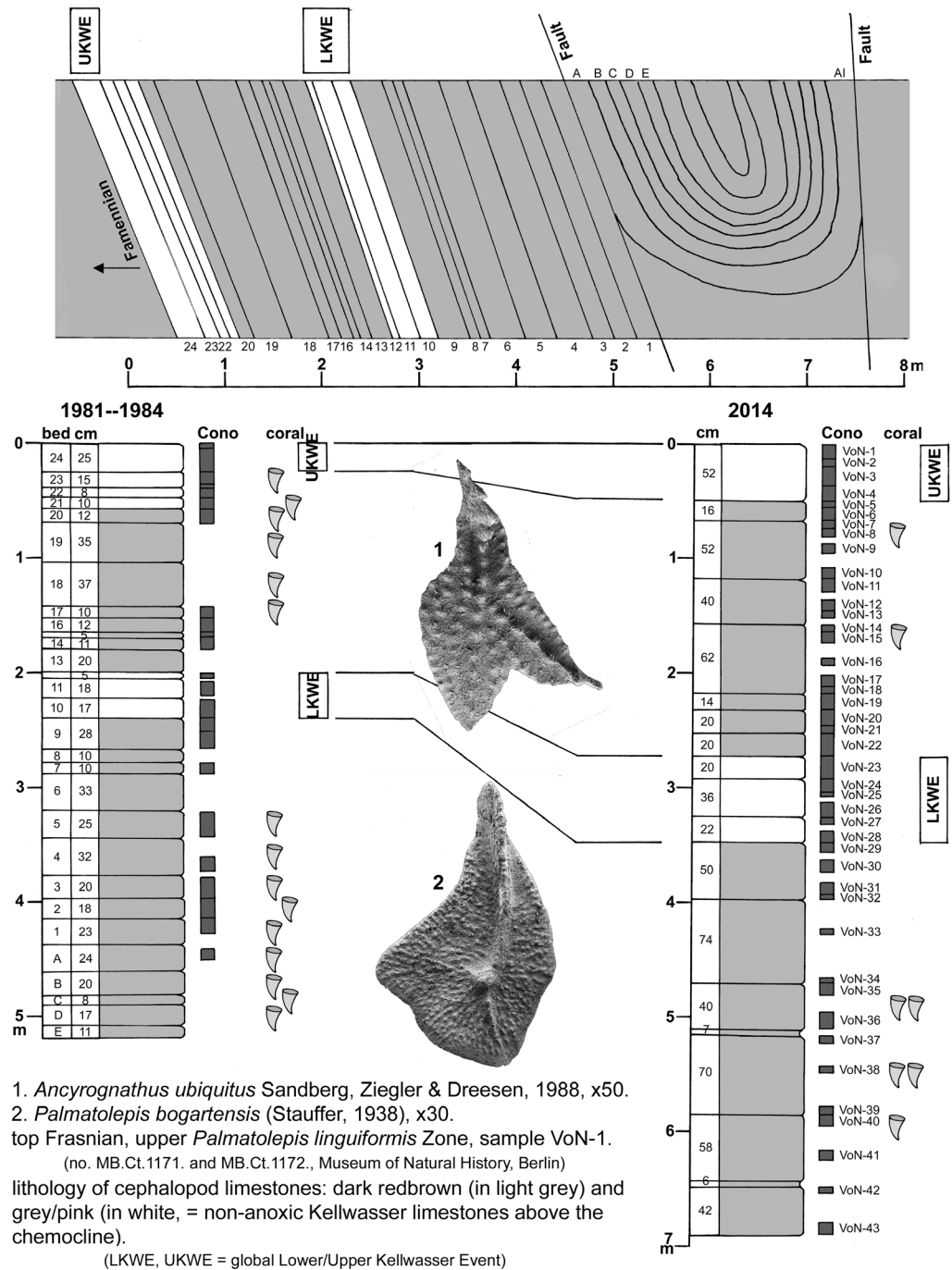
The Frasnian section (Fig. 3) offers two levels with rich Rugosa associations. The upper one (between the two Kellwasser Events) is dated as Upper *Palmatolepis rhenana* Zone and Lower *Palmatolepis linguiformis* Zone. The lower one (beds D-5, below the Lower Kellwasser Event) represents most probably the Lower *Palmatolepis rhenana* Zone. *Palmatolepis rhenana rhenana* Bischoff, 1956, the index fossil of the Upper *Palmatolepis rhenana* Zone, was observed in beds 7 and 9.

The Rugosa fauna (about 400 specimens, coll. D. Weyer 1983–1984) is nearly the same as that from the Geipel quarry in Schleiz, and in even better preservation. *Metriophyllum* Milne-Edwards & Haime, 1850 (in the sense of Weyer (1991, 1996) – according to a prepared revision by Rohart & Weyer) is the characteristic genus. The new taxon *Spinaxon potyi* dominates with 109 specimens in the earlier beds below the Lower Kellwasser Event; the younger community in beds between the two Kellwasser Events yielded only two specimens.

#### 2.5. Baltic Sea island Rügen

The Frasnian shallow water shelf sections of Rügen yield solitary Rugosa (genus *Metriophyllum* Milne-Edwards & Haime, 1850 – Zagora & Aehnel, 2009, p. 161, fig. 1) in their deeper facies

**Figure 3.** Upper Frasnian section of Vogelsberg quarry NNE of Göschitz (Bartzsch and Weyer in 1981-1984, 2014, unpublished), with the two non-anoxic Kellwasser Limestone horizons – outcrop situation of 1981-1984 (above and left, partly still preserved as nearly inaccessible steep quarry wall), and of 2014 in a deeper quarry level (first undisturbed complete Vogelsberg Formation with basal contact to the diabase volcanites of the Görkwitz Formation) – source of rich ahermatypic Rugosa faunas between the two Kellwasser Events (Upper *Palmatolepis rhenana* Zone, Lower *Palmatolepis linguiformis* Zone), and below the Lower Kellwasser Event (Lower and Upper *Palmatolepis rhenana* Zones).



1. *Ancyrognathus ubiquitous* Sandberg, Ziegler & Dreesen, 1988, x50.  
2. *Palmatolepis bogartensis* (Stauffer, 1938), x30.  
top Frasnian, upper *Palmatolepis linguiformis* Zone, sample VoN-1.  
(no. MB.Ct.1171. and MB.Ct.1172., Museum of Natural History, Berlin)  
lithology of cephalopod limestones: dark redbrown (in light grey) and grey/pink (in white, = non-anoxic Kellwasser limestones above the chemocline).  
(LKWE, UKWE = global Lower/Upper Kellwasser Event)

of Matagne type. I collected (1970-1974) all the materials from the available core of four deep boreholes. The coral faunas are stored in the Bundesanstalt für Geologie und Rohstoffe, Berlin Department (BGR.Berlin).

In the northwestern part of the island of Rügen, the Matagne facies occurs only in the Late Frasnian (Upper *Palmatolepis rhenana* Zone, lithostratigraphic unit 9a – Zagora & Aehnelt, 2009):

Borehole Wiek 4 1969 (core 2385.0–2394.0 m; Zagora & Aehnelt 2009: 178, section 6): *Metriophyllum* sp. >20 mostly fragmentary small solitary Rugosa.

Borehole Dranske 2 1970 (core 2625.2–2634.3 m; Zagora & Aehnelt, 2009, p. 176, section 4): *Metriophyllum* sp. (Fig. 4 B1-3, sometimes settled by Auloporidae).

Borehole Neuenkirchen 1 1972 (core 3009.0 – 3019.0 m; Zagora & Aehnelt, 2009, p. 101, section 9): *Metriophyllum* sp.

In the southeastern part of the island of Rügen, the Matagne facies starts already in the Early Frasnian (*Palmatolepis punctata* Zone, lithostratigraphic units 1a and 1'a – Zagora & Aehnelt, 2009, p. 185, section 13):

Borehole Binz 1 1973 (core 2872.5 – 2877.0 m = lithostratigraphic unit 1a; cores 3035.0 – 3044.0 m and 3058.0 – 3075.1 m = lithostratigraphic unit 1'a): *Metriophyllum* sp. (Fig. 4 A1-6), *Metrioplexus* sp.

### 3. Taxonomy

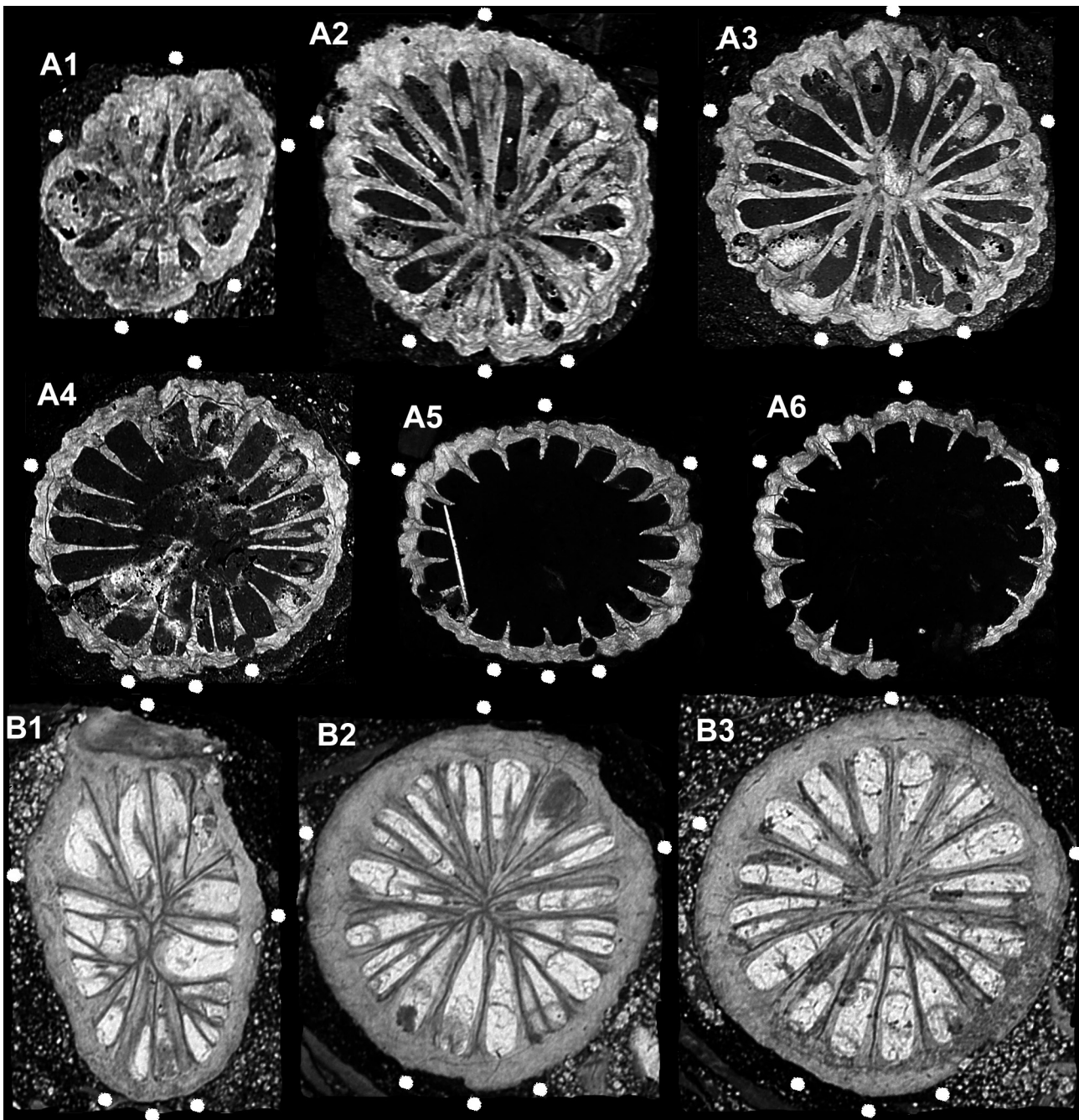
The following abbreviations are used (especially in septal formulae): n = number of major septa, N = number of all (major and minor) septa, D = diameter, CS = transverse (cross) section, LS = longitudinal section, TS = thin section, P = peel, R = remaining piece of corallum. Six protosepta are marked in the transverse sections (cardinal septum at top); all illustrations are presented as seen from above into the calice.

Superorder Rugosa Milne-Edwards & Haime, 1850

Order Stauriida Verrill, 1865

Suborder Cyathaxoniina Spasskiy, 1977

*Remarks.* This taxon is named *Metriophyllina* Spasskiy, 1965 in our classical Rugosa handbook (Hill, 1981, p. F186). Later revisions – not yet published (Rohart & Weyer, in preparation), but first mentioned in Weyer (1991, p. 11, 1996, p.



**Figure 4.** Frasnian *Metriophyllid* Rugosa from the Baltic Sea island of Rügen. A1-6. *Metriophyllum* sp. 1, lower Frasnian, borehole Binz 1 1973, depth 3036.2 m, coll. D. Weyer 1974 (BGR.Berlin X13224.), ontogenetic series of six calicular cross sections, x15 (A1), x12 (A2), x9 (A3), x8 (A4), and x6 (A5-6); – catasepta (excepting those of the antiseptial triad) in the highest calicular section A6 already reduced and incorporated into the stereoplastic thickened archaeotheca, visible only as external longitudinal septal furrows. B1-3. *Metriophyllum?* sp. 2, upper Frasnian, borehole Dranske 2 1970, depth 2625.7 m, coll. D. Weyer 1971 (BGR.Berlin X13223.); three subtabular cross sections, x15 (missing antiseptial minor septa triad does not correspond to the diagnosis of the genus *Metriophyllum*).

85) – resulted in drastic changes, because the real *Metriophyllum* Milne-Edwards & Haime, 1850 is a member of the suborder Stereolasmatina Hill, 1981 (= *Zaphrentoidina* Schouppé & Stacul, 1959) and its family Stereolasmatidae Fomichev, 1953, a junior synonym of *Metriophyllidae* Hill, 1939, which also will become a junior synonym of *Lindstroemiidae* Počta, 1902 (*Lindstroemia* Nicholson & Thomson, 1876 is a senior synonym of *Lopholasma* Simpson, 1900). The main representatives of this suborder are the *Cyathaxoniidae* Milne-Edwards & Haime, 1850, which include the *Laccophyllinae* Grabau, 1928 as immediate ancestor of the *Cyathaxoniinae* (lower Famennian–Lower Permian). The true, completely aseptal columella of *Cyathaxonia* Michelin, 1847 is nothing but the everted aulus of *Laccophyllum* Simpson, 1900 (Weyer, 1996, p. 85, 2001, p. 73). A trend (*sensu* Lang, 1923), seen in many Rugosa groups – trend towards contraclin contratingent catasepta and biform

tabularium (often both features are closely connected) – occurs in the *Cyathaxoniina*, too: genera around *Petraia* Münster, 1839 and *Neaxon* Kullmann, 1965. Curiously, at first the contratingent structure was seen as the primitive (plesiomorph) septal plan (Schindewolf, 1931, 1942), but in fact the phylogeny was running in the opposite direction. Since a real cladistic classification (contratingent structure independently developed in various lineages) is not yet elaborated, such ancestral genera of the suborder are provisionally grouped as *Petraiidae* de Koninck, 1872 for the moment. Present knowledge is still too imperfect to allow better proposals for a natural classification; ahermatypic Rugosa seem to appear in Wenlock Ludlow times, but there is the outstanding misfit *Protozaphrentis* Yü, 1957 of presumed early Upper Ordovician age, with a well developed apomorphic contratingent septal arrangement.

## Family Petraiidae de Koninck, 1872

*Remarks.* We have no reliable subfamily subdivision of the included genera, classified by Hill (1981) as Neaxoninae Hill, 1981, Friedbergiinae Rózkowska, 1969, Guerichiphyllinae Rózkowska, 1969, and Amplexocariniinae Soshkina, 1941. In addition, the Bathyalvinae Weyer, 1991 had been proposed. The generally accepted revision of *Petraia* Münster, 1839 by Schindewolf (1931) is unacceptable (Weyer, 1980), as it did not rely on the original syntypes and defined the genus by a coral not present in the Münster collection, later renamed *Muenstraia* Weyer, 2001.

A special problem is due to the genera with dissepiments: *Czarnockia* Rózkowska, 1969, *Hillaxon* Rózkowska, 1969, *Catactotoechus* Hill, 1954, *Nicholsoniella* Soshkina, 1952, *Guerichiphyllum* Rózkowska, 1969, *Alborziphyllum* Ashouri, Abbasi & Khaksar, 2010. For the moment they are still united in a presumably artificial manner as the Guerichiphyllinae Rózkowska, 1969. The pleonophorous structure (Rugosa with dissepiments, Dybowski, 1873) is often declared *ex cathedra* as a feature of family subfamily rank in taxonomy – such an old-fashioned procedure would be a typical “horizontal” classification not reflecting true phylogenetic lines. Monotypic taxa of the family group (subtribus – superfamily) are inadequate, therefore authors included dissepimental genera into mainly non-dissepimental subfamilies or *vice versa* (Hill, 1981: *Catactotoechus* Hill, 1954 in Neaxoninae; Berkowski, 2006: *Vesiculolasma* Berkowski, 2006 in Sutherlandiniinae; Weyer, 2001: *Schindewolfia* Weissermel, 1943 in Taralasmatinae).

## Subfamily Petraiinae de Koninck, 1872

Synonym: Neaxoninae Hill, 1981.

*Genera included.* *Neaxon* Kullmann, 1965, *Paliaxon* Weyer, 1981, *Neaxonella* Weyer, 1978, *Neosyringaxon* Jia, 1977, *Erfoudia* Berkowski, 2008, *Accurganax* Li, 1979 (?synonym *Marocaxon* Berkowski, 2008), *Petraia* Münster, 1839, *Spinaxon* gen. nov., *Nalivkinella* Soshkina, 1939, *Gorizdronia* Rózkowska, 1969.

Genus *Spinaxon* gen. nov.

*Type species.* *Spinaxon potyi* sp. nov.

*Etymology.* For the exaggerated trabicular septal spines in the aulos.

*Diagnosis.* *Neaxon*-like small long-conical corals with coarse monacanthine trabicular microstructure (multitrabicular only at the upper calicular margin). Cardinal septum as long as other major septa, also in calicular stages never shortened. Aulos (circulotheca) complete and mostly well developed, in mature stages often disappearing and reappearing during ampleximorph phases. Tabulae slightly domed. Radially arranged major septa outside the aulos at the calicular base with trabiculae fused to form platy septa, which bear inside the aulos extremely long thick trabicular spines often nearly reaching the centre, where they can bend upward nearer to a vertical growth direction. Their appearance within the circulotheca sometimes resembles an axial structure, but no real evert calicular boss can be observed. Minor septa are extremely short, sometimes obscure or apparently missing due to their spiny inner margin; no antiseptal triad.

*Comparison.* The ancestors of *Spinaxon* are the two closely related genera *Neaxon* (with complete circulotheca throughout growth) and *Petraia* (circulotheca incomplete in mature stages). The excessively elongated trabicular spines at the septal margin of major septa are the distinctive feature of the new genus – these spines enter the circulotheca (*sensu* Fedorowski, 2009) up to its centre. Such a structure never appears in *Neaxon* throughout its at least Lochkovian–top-Famennian lifespan, and also never in its descendant *Petraia* (for the moment known for certain only from Frasnian–Famennian times, but probably arising earlier).

*Occurrence.* At present, monotypic in the Upper Frasnian, Thuringia (Germany) and Montagne Noire (France). It is still unknown whether *Spinaxon* evolved only during the Frasnian or earlier in the Middle or even Lower Devonian.

*Spinaxon potyi* sp. nov.

Figs 5-6-7, Table 1, Pl. 1-4

2003 nov. gen. nov. sp. II; Weyer et al., 76, fig. 2E, F.

*Etymology.* Dedicated to Edouard – Eddy – Poty, on occasion of his 65<sup>th</sup> birthday, and in recognition of his intensive studies of Upper Devonian – Lower Carboniferous Rugosa.

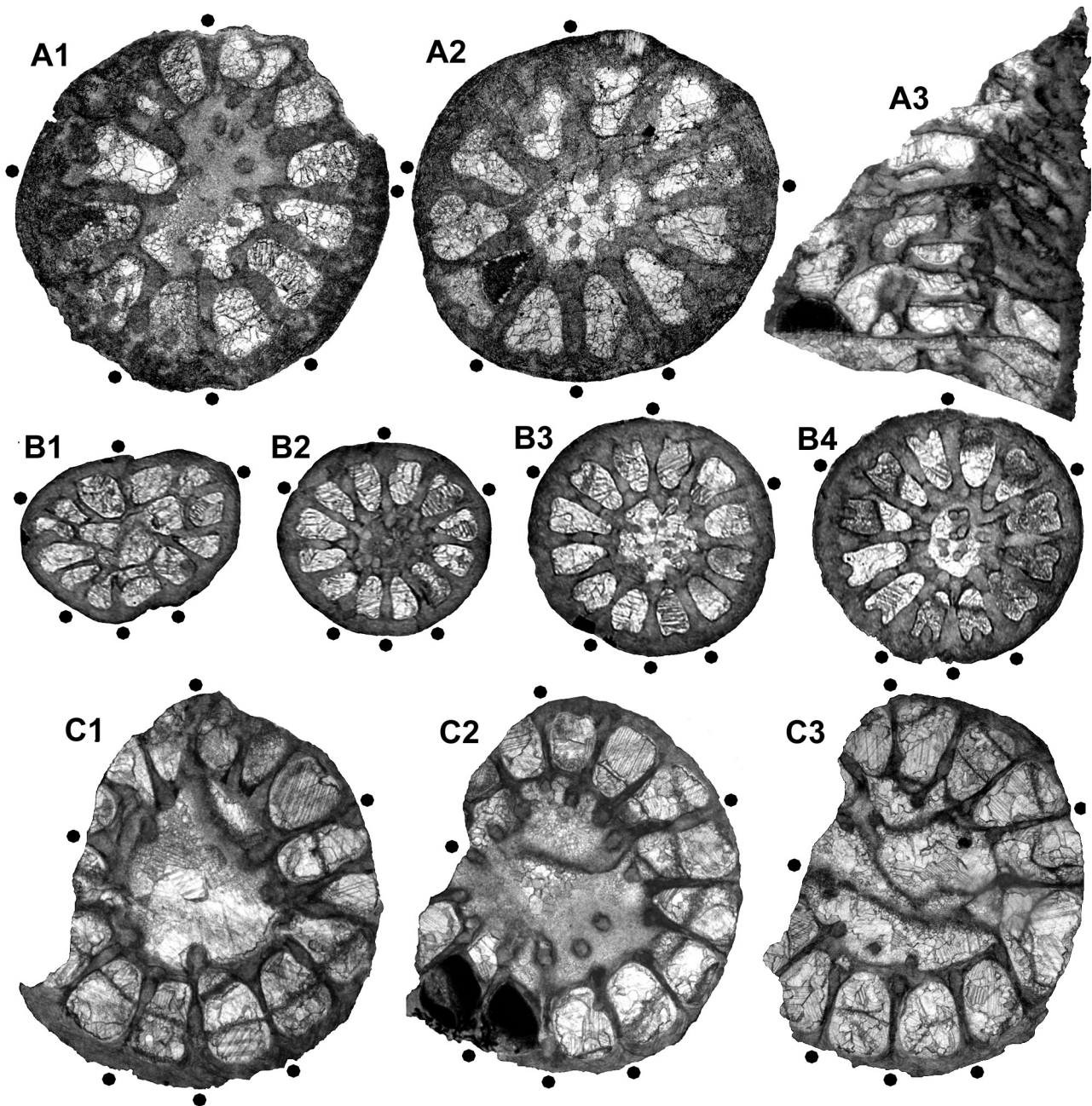
*Holotype.* specimen MB.K.7957 = 4 CS (1P, 3TS), 4 LS (TS) – Fig. 7 A1-4, Pl. 1 G1-5.

*Type locality.* Vogelsberg quarry 1 km NNE of Göschitz (NNE of Schleiz).

*Type horizon.* Cephalopod limestone of the middle Vogelsberg Formation (bed A, Fig. 3, left section) – upper Frasnian, Lower

specimen	figures	septal formula	n	N	D (mm)
MB.K.7949	Fig. 6 A1-A2	$\frac{3}{3} \frac{3}{3}$	16	24	3.8
MB.K.7949	Fig. 6 A3-A4	$\frac{2}{3} \frac{3}{3}$	15	22	3.8-3.9
MB.K.7953	Fig. 6 B1	$\frac{3}{4} \frac{2}{4}$	17	26	3.6
MB.K.7953	Fig. 6 B2-B3	$\frac{3}{4} \frac{3}{5}$	19	30	4.3-4.5
MB.K.7957	Fig. 7 A1	$\frac{3}{3} \frac{3}{3}$	16	24	3.5
MB.K.7957	Fig. 7 A2-A4	$\frac{3}{4} \frac{3}{4}$	18	28	3.9-5.2
MB.K.7956	Pl. 3 A1-A2	$\frac{2}{4} \frac{2}{4}$	16	24	3.2-3.6
MB.K.7956	Pl. 3 A3	$\frac{3}{4} \frac{2}{5}$	18	28	4.8
MB.K.7956	Pl. 3 A4-8	$\frac{3}{5} \frac{2}{5}$	19	30	6.0-6.4
MB.K.7962	Pl. 3 C1	$\frac{2}{4} \frac{2}{4}$	16	24	3.6
MB.K.7962	Pl. 3 C2	$\frac{2}{5} \frac{2}{5}$	18	28	5.6
MB.K.7961	Pl. 3 D1	$\frac{2}{5} \frac{2}{5}$	18	28	4.3
MB.K.7961	Pl. 3 D2-D4	$\frac{4}{5} \frac{3}{5}$	21	34	9.7-7-7
MB.K.7954	Pl. 4 A1	$\frac{2}{3} \frac{3}{3}$	15	22	2.7
MB.K.7954	Pl. 4 A2-A3	$\frac{3}{3} \frac{3}{3}$	16	24	3.8-4.4

Table 1. Septal formulae of selected specimens.



**Figure 5.** *Spinaxon potyi* sp. nov., paratypes, Thuringia. A1-3. MB.K.7949, former Geipel quarry in Schleiz, upper Vogelsberg Formation, bed 4A, Upper Frasnian, top of Upper *Palmatolepis rhenana* Zone, coll. D. Weyer 1995; A1, 2. subtabular cross sections, (nos 8, 5), x15, A3. median longitudinal section (no. 1), x12 (drawings see Fig. 6 A1-4). B1-4. MB.K.7950, former Geipel quarry in Schleiz, upper Vogelsberg Formation, bed 4B, Upper Frasnian, boundary of top Upper *Palmatolepis rhenana* Zone and Lower *Palmatolepis linguiformis* Zone, coll. D. Weyer 1995; subtabular cross sections, x10. C1-3. MB.K.7953, former Braunsberg quarry ESE Tegau, upper Vogelsberg Formation (loose block), Upper Frasnian, Lower-Upper *Palmatolepis rhenana* Zones, coll. D. Weyer 1966; subtabular cross sections (nos 5, 4, 3), x15 (C1) and x12 (C2, 3) (drawings see Fig. 6 B1-3).

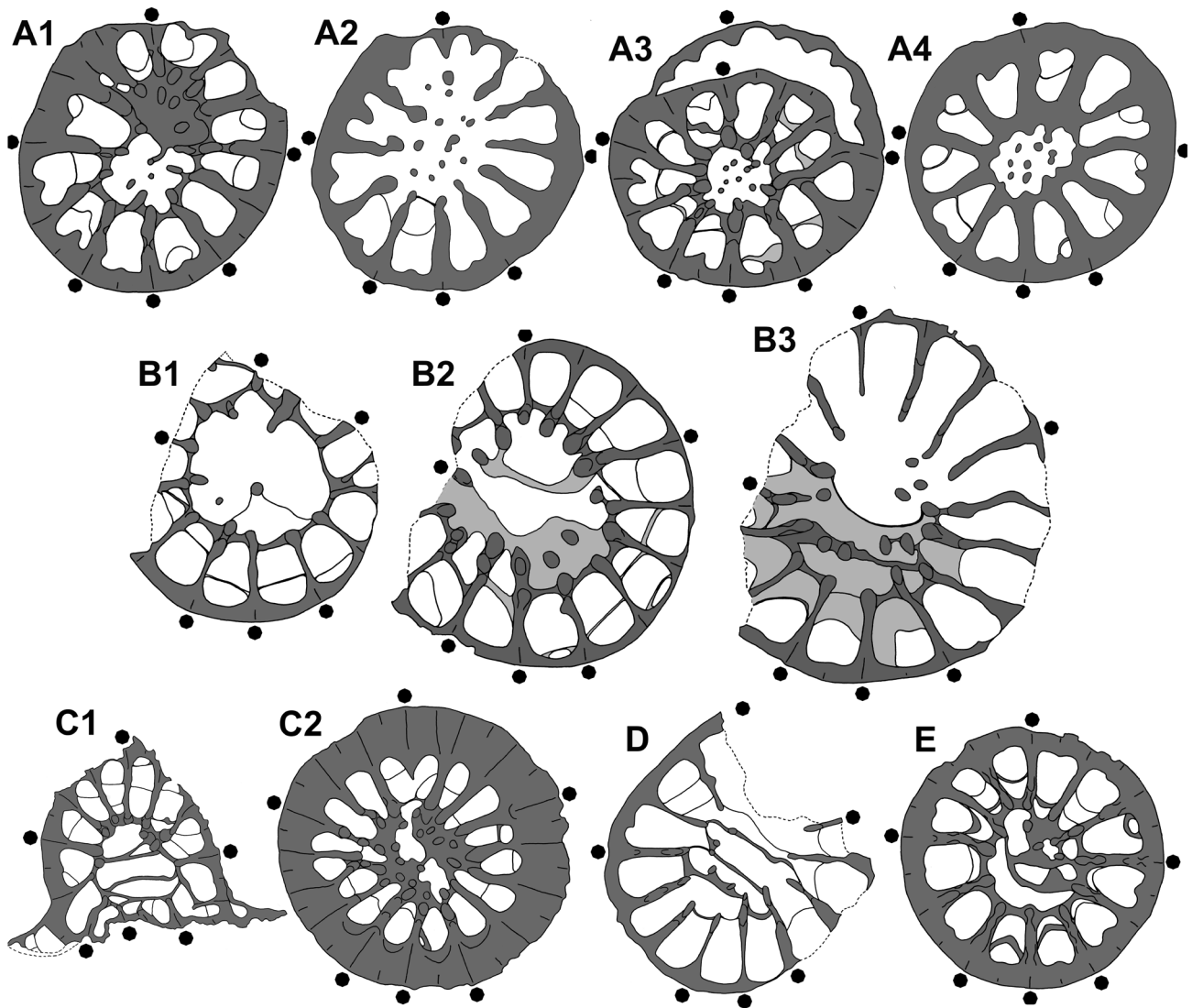
#### Upper *Palmatolepis rhenana* Zone.

**Material.** 117 specimens from four localities in Germany (Thuringia) and from one locality in France (Montagne Noire). 241 thin sections (209 cross, 32 longitudinal) have been prepared from 40 specimens. 77 specimens were only cut and studied with at least one polished and HCl-etched surface showing the long trabecular spines within the circulotheca. The collection is stored in the Museum of Natural History (Leibniz Institute) at the Humboldt University in Berlin (numbers MB.K.7949-7995), except four specimens from Vogelsberg quarry donated to the University of Liège (Collections de Paléontologie animale et humaine, numbers ULg.2015-05-22 1, 2, 3, 4). A geographic map of the Thuringian localities was given by Bartzsch et al. (1993, p. 6).

Vogelsberg quarry NNE of Göschitz – 111 specimens: The extremely rich collection was sampled from the older left Upper

Frasnian section in 1983-1984 (Fig. 3), now partly vanished and partly inaccessible at the steep WSW wall of the quarry. The great majority (109 *Spinaxon*) occurred below the Lower Kellwasser Event: bed 4 (2), bed 3 (16), bed 2 (43), bed 1 (1), bed A (10), Bed B (11), Bed C (1), Bed D (1), bed AI (23), loose pebble (1). Only 2 *Spinaxon* were found just below the Upper Kellwasser Event (undivided sample of beds 23–20, Fig. 1 – MB.K.7987.1-2). The illustrated specimens are: MB.K.7955 = 2CS (TS), 1LS (TS) – bed B – Pl. 1 B1-3; MB.K.7956 = 11CS (5P, 6TS), 1R – bed A – Pl. 1 A1-5, 3 A1-9; MB.K.7957 = 4CS (1P, 3TS), 4LS (TS) – bed A – Fig. 7 A1-4, Pl. 1 G1-5, holotype; MB.K.7958 = 9CS (3P, 6TS), 2LS (TS) – bed 1 – Pl.2 D1-3; MB.K.7959 = 6CS (4P, 2TS), 1R – bed 3 – Pl. 1 f, 3 B1-3; MB.K.7960 = 11CS (5P, 6TS), 2LS (1P, 1TS) – bed 2 – Fig. 6 C1-2, Pl. 4 D1-3; MB.K.7961 = 10CS (7P, 3TS), 2LS (TS) – bed B – Pl. 1 D1-2, 3 D1-4; MB.K.7962 = 3CS (2P, 1TS), 7LS (5P, 2TS) – bed 3 – Pl. 1 E1-2, 3 C1-5; MB.K.7963 = 7CS (3P, 4TS), 2R – bed 2 – Fig.





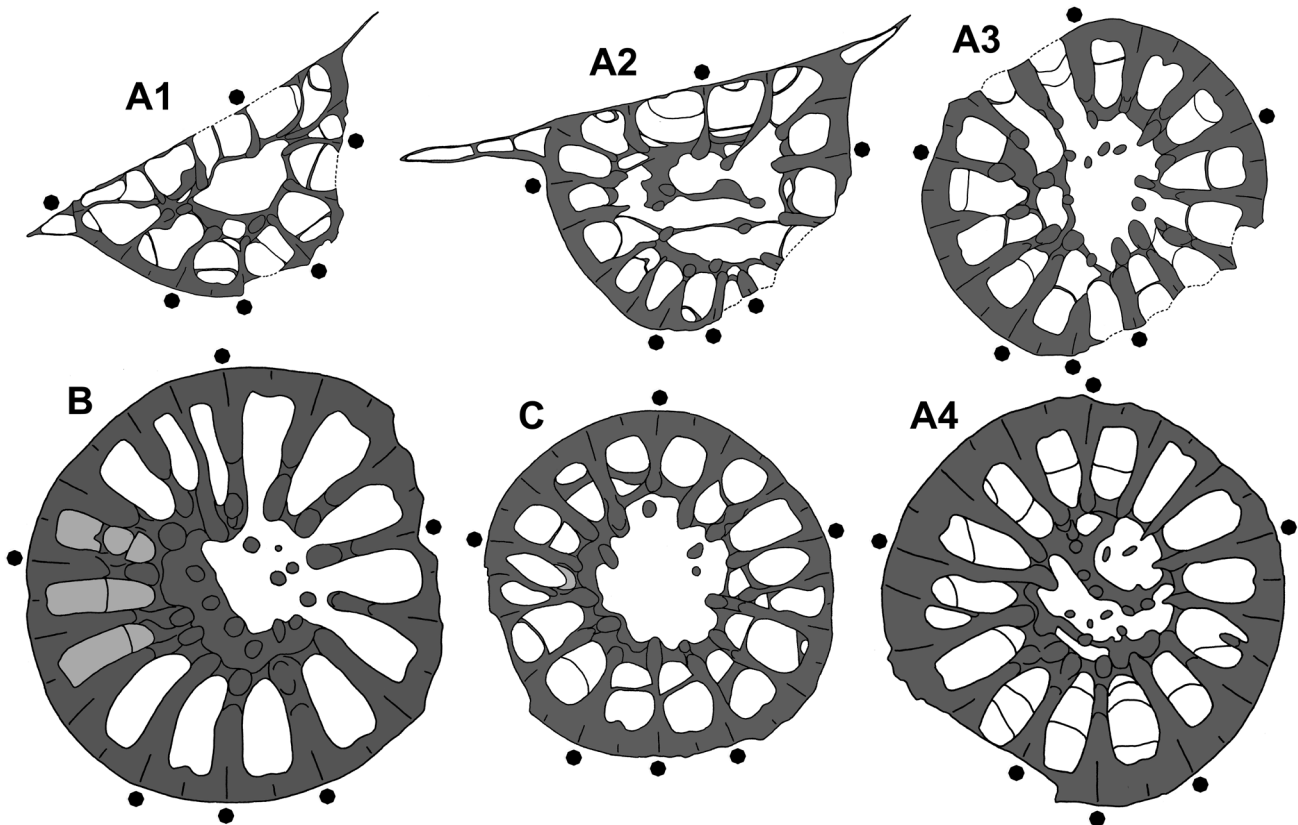
**Figure 6.** *Spinaxox potyi* sp. nov., paratypes, Thuringia and Montagne Noire. A1-4. MB.K.7949, former Geipel quarry in Schleiz, upper Vogelsberg Formation, bed 4A, Upper Frasnian, top of Upper *Palmatolepis rhenana* Zone, coll. D. Weyer 1995; subtabular cross sections (nos 9, 7, 6, 5), x10, in A2 with mature ampleximorph phase, in A3 with rejuvenescence (photos see Fig. 5 A1-3). B1-3. MB.K.7953, former Braunsberg quarry ESE Tegau, upper Vogelsberg Formation (loose block), Upper Frasnian, Lower-Upper *Palmatolepis rhenana* Zones, coll. D. Weyer 1966; subtabular cross sections (nos 6, 4, 2), x10 (photos see Fig. 5 C1-3). C1-2. MB.K.7960, Vogelsberg quarry NNE of Göschitz, upper Vogelsberg Formation, bed 2, Upper Frasnian, probably Lower *Palmatolepis rhenana* Zone, coll. D. Weyer 1983-1984; subtabular cross sections (nos 12, 4), x 7 (C1) and x6 (C2) (photos see Pl. 4 D1-3). D. MB.K.7952, former Kahlleite quarry SW of Rödersdorf, upper Vogelsberg Formation (loose block 14), Upper Frasnian, Lower or Upper *Palmatolepis rhenana* Zone, coll. D. Weyer 1985; subtabular cross section (no. 1), x6 (photos see Pl. 4 B1-3). E. MB.K.7954, upper Coumiac quarry near Cessenon, bed 31b, Lower *Palmatolepis linguiformis* Zone, coll. R. Feist 1992; subtabular cross section (no. 4), x10 (photos see Pl. 4 A1-3).

7 B, Pl. 1 C1-2; MB.K.7964 = 5CS (TS), 2LS (TS) – bed AI – Pl. 2 A1-4; MB.K.7965 = 2CS (TS), 2LS (TS) – bed 2 – Fig. 7 C, Pl. 2 C1-3; MB.K.7966 = 5CS (TS) – bed 3 – Pl. 2 B1-5; Further specimens thin-sectioned, but not figured are numbered MB.K.7967-7986; specimens studied only with polished-etched surfaces bear the numbers MB.K.7987-7995 (with sub-numbers). Geipel quarry in Schleiz – two specimens: MB.K.7949 = 6CS (4P, 2TS), 3LS (1P, 2TS) – Fig. 5 A1-3, 6 A1-4; MB.K.7950 = 4CS (TS), 1R – Fig. 5 B1-4. Kahlleite quarry SW of Rödersdorf – two specimens: MB.K.7951 = 5CS (TS) – Pl. 4 C1-3; MB.K.7952 = 6 CS (TS), 1R – Fig. 6 D, Pl. 4 B1-3. Braunsberg quarry ESE of Tegau – one specimen: MB.K.7953 = 6CS (TS) – Fig. 5 C1-3, 6 B1-3. Coumiac upper quarry near Cessenon – one specimen: MB.K.7954 = 6CS, 1R (and 2CS of another attached *Rugosa*) – Fig. 6 E, Pl. 4 A1-3. Frasnian-Famennian stratotype section, bed 31b, Lower *Palmatolepis linguiformis* Zone, collected by Raimund Feist in 1992. The outcrop is described in Becker & House (1994, p. 51, indicating the presence of solitary *Rugosa* corals in beds 31c2 and 31e2) and in House et al. (2000). One accompanying *Rugosa* in bed 31b is *Metriophyllum* sp.; one further coral from bed 31 (without more detailed origin) is a *Metrioxox* sp.

*Diagnosis.* Until the discovery of further species – identical with the actual diagnosis of the monotypic new genus.

*Description.* The small, long conical, mostly straight (excepting the talon curvature) or slightly cornute corals reach a length of 12–20 mm and a calicular diameter of 4–9 mm. The larval phase started mostly with a horizontal talon fixed to any hard ground; often rejuvenescence occurred during later vertical growth. The smallest observed diameter was 2.5 mm (with already 22 septa and an aulos – Pl. 4 A1). Size of talon may amount to 6 mm. The depth of calice is somewhat smaller than its diameter. The archaeotheca bears only growth rugae; longitudinal ribbing could not be seen. The cardinal septum of cornute coralla prefers the convex side (according to the talon position (Fig. 7 A2, Pl. 1 G2, 4 A1) as in the ancestral genus *Neaxox*; an opposite orientation on the concave side is rare (Fig. 6 C1, Pl. 2 B2).

The adult septal apparatus comprises 28 septa; here a cardinal quadrant contains one or three less major septa than a counter quadrant (Fig. 7 A4, Pl. 3 C2). Often, an earlier phase occurs with equal number of major septa in every quadrant (Fig. 6 A2, total



**Figure 7.** *Spinaxton potyi* sp. nov., holotype and paratype, Thuringia, Vogelsberg quarry NNE of Göschitz, upper Vogelsberg Formation, probably Lower *Palmatolepis rhenana* Zone, coll. D. Weyer 1983-1984. A1-4. MB.K.7957, holotype, bed A, subtabular cross sections (nos 8, 7, 6, 3), x10 (photos see Pl. 1 G1-5). B. MB.K.7962, paratype, bed 2, cross section (no.2) at calicular base (subtabular regions in light grey), x10 (photos see Pl. 1 C1-2). C. MB.K.7965, paratype, bed 2, subtabular cross section (no. 6), x12 (photos see Pl. 2 C1-3).

septal number 24). Specimens with a diameter >6 mm (exception Fig. 6B) may construct 30 septa (Pl. 3 A7); the observed maximum is 34 septa (Pl. 3 D4). The youngest available stage (Pl. 2 B1) still within the talon region has 20 septa. All the major septa – of course excepting the last one of every quadrant – are of equal length and unite in the lower calice to form an aulos. This circulotheca starts very early already in the talon phase and is formed as a separate interior wall by everted tangential wall pieces (with a dark median line) between the axial major septa ends – there is no basal dark line as in tabulae. The aulos is quite permanent and attains about one third of the corallum diameter in juvenile and middle growth stages, often enlarging in the mature stage to one half of the corallum diameter. There an ampleximorph trend is generally distributed, starting with local disappearance of interior wall pieces between several major septa (Fig. 5 C3), and leading to a complete loss of any aulos structures (Fig. 6 D, Pl. 2 B5, C1). Occasionally, intersections of tabulae (with a basal dark line) can imitate local parts of an aulos wall during the ampleximorph phase. Sometimes (especially after rejuvenescence), the complete circulotheca may reappear (Figs 6 A1-4, 7 A3-4).

The septal microstructure is coarsely monacanth, besides a short phase of multitrabular septal margins immediate at the upper calicular rim (Pl. 3 A9) – as in the ancestral group around the genus *Neaxon* (Weyer, 1971, 1984a). The spiny margin of a major septum outside the aulos is clearly visible in Pl. 1 G4. Fusion of the rather long trabiculae to form a platy septum occurs by comparatively thin stereoplasmatic deposits, causing typical undulated view of swelling up and down intersections in both transverse and longitudinal sections (Fig. 5 C1-3, Pl. 2 C2). Due to missing recrystallizations, the original spiny structure is well visible (Pl. 4 D1-3). Within the circulotheca, the trabicular spines grow extremely long, remain totally unfused, and are bending up to a more and more nearly vertical orientation (Pl. 2 C1, D1-2). They seem to suggest an axial structure (Pl. 2 A3), but there is no everted axial boss (Pl. 1 C2, G4). These exaggerated trabicular spines of the central region disappear during an ampleximorph

phase (Pl. 2 B5, C1).

Minor septa are extremely short and of equal length (no preferred growth near the antiseptum). Their occasional “absence” within the calicular lumen (Pl. 1 D2) is due to a transverse cut just between two trabicular spines. Many subtabular cross sections show no active minor septa: they have been reduced by continuous stereoplasmatic thickening of the archaeotheca during the calyx ontogenesis, but remain well visible now hidden within the wall. In cases of stronger recrystallization, such structures had been misinterpreted as a late (“zaphrentoidid”) cyclic insertion of minor septa, which does not exist among *Rugosa* with their always serial (“cyathaxoniid” = retroserial) insertion mode.

Identification of six (or four) protosepta is not easy and requires an ontogenetic series of cross sections. They may offer phases at the four insertion points with major septa, not yet grown to full length and inclined towards (or even attached to) the neighbouring antiseptal major septum (Pl. 2 B4, C3). The cardinal septum is never shortened, even in the higher calice (Pl. 1 D2, 3 A5-9). Apparent opposing pictures (Fig. 5 C1-3, 7 C, Pl. 3 D3) represent incidental cuts just between two trabicular spines in a cross section.

A well developed convex tabularium consists of prevailing simple tabulae (and rare tabellae) in various inclination, from mostly sloping down to the wall at about 45° to sometimes even horizontal (Pl. 1 E2), outside the elevated circulotheca (Pl. 3 C4-5). Inside the aulos, flat or slightly domed tabulae and also many tabellae are typical, often thickened by stereoplasma. The peripheral tabulae remain thin. There is no fossular structure. Criteria of a biform tabularium are absent: though sometimes tabulae intersections cross interseptal lumina not in tangential directions, but oblique (distance from the wall greater at the cardinal side of one lumen than at the antiseptal side, Fig. 6 B1-2) or without touching at the antiseptal side of one lumen (Fig. 6 A1, 4). Such structures are not regularly distributed over all the quadrants (Fig. 7 A4, C, with occasional opposite tabulae course).

*Variability.* The rich available material allowed numerous illustrations in order to demonstrate the intraspecific variations. This is also needed for other small ahermatypic corals like *Cyathaxonia* Michelin, 1847, *Laccophyllum* Simpson, 1900, or *Neaxon* Kullmann, 1965, the species of which are often very similar and generally without clearly visible morphological differences.

Early ontogenesis demonstrates a common position of the cardinal septum at the convex side of the talon, a heritage from the ancestral genus *Neaxon*, but rarely an opposite position at the concave side was also observed. After the talon fixation on a hard object, the coral preferred a straight vertical growth; there are only few slightly cornute specimens, but no completely and regularly cornute coralla throughout their total length.

The comparison of the somewhat older rich collection (112 specimens) from the level below the Lower Kellwasser Event with the few (5 specimens, 3 of them illustrated) younger specimens from horizons below the Upper Kellwasser Event did not indicate specific differences. Only one common feature of the younger group, the slightly greater length of the subtabular mostly present minor septa (Figs 5 A, B, 6 A, E), might perhaps be of some significance, but this can not be judged on the basis of such restricted material.

The older population of the Vogelsberg quarry varies in the inclination of the peripheral tabulae – this can be observed in one and the same specimen (Pl. 1 E1-2, 2 C1). The adult ampleximorph trend is missing, weakly indicated, or extremely developed. Its start is seen in specimens with major septa of still normal length, not longer united axially by a complete circulotheca, but ending free around the centre or connected only by tabulae (Fig. 5 C3, 6 A2, D). Axial trabeculae found within the aulos of transverse sections are numerous (Fig. 6 A3-4, Pl. 1 A4, 2 D3) or few and situated only in the outer circle of the aulos (Fig. 6 B1-2, 7); this is partly related to the position of the section immediately upon a tabula or at different distances above a tabula.

*Occurrence.* As for genus.

#### 4. Acknowledgments

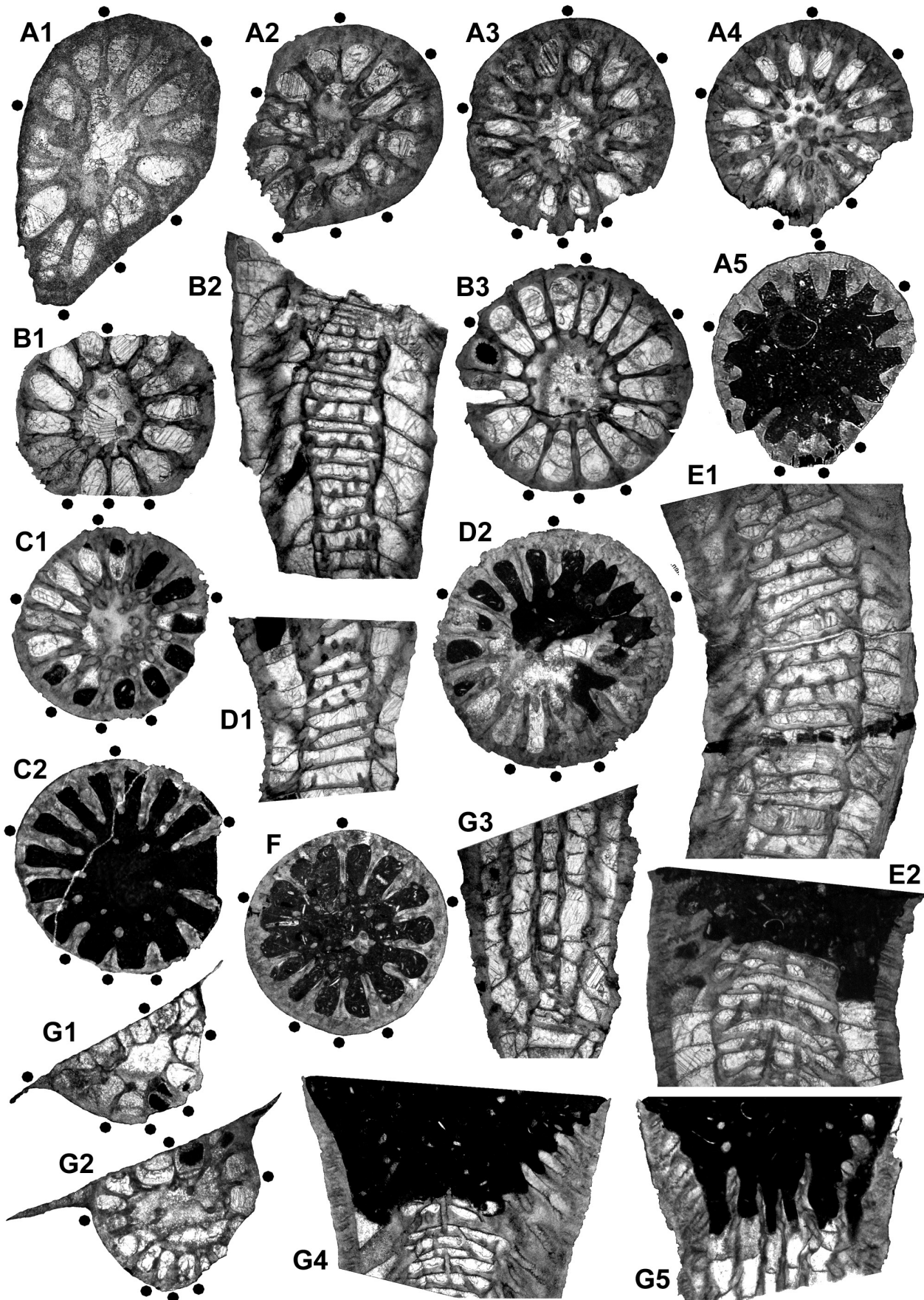
Konrad Bartsch (Saalfeld) always assisted during field work in Thuringia (1981-1983) and conodont sampling. Birgit Gaitzsch (Freiberg) improved our new section of 2014 by her sedimentological studies. Jean-Jacques Cornée and Catherine Girard (Montpellier) discussed during an excursion in 2015 the unique non-anoxic Kellwasser Event horizons of the Vogelsberg quarry. Gilbert Klapper (Iowa City) controlled determinations of Frasnian *Palmatolepis* species. Raimund Feist (Montpellier) donated his coral collection from the global stratotype of the Frasnian–Famennian boundary at Coumiac in 1995. Ilona Schäpan (Potsdam) provided the REM photos of conodonts. Ross McLean (Forrester's Beach) and Tomasz Wrzolek (Sosnowiec) improved the first draft of the manuscript by their critical and linguistic reviews. My sincere thanks go to all of them for their kind help.

#### 5. References

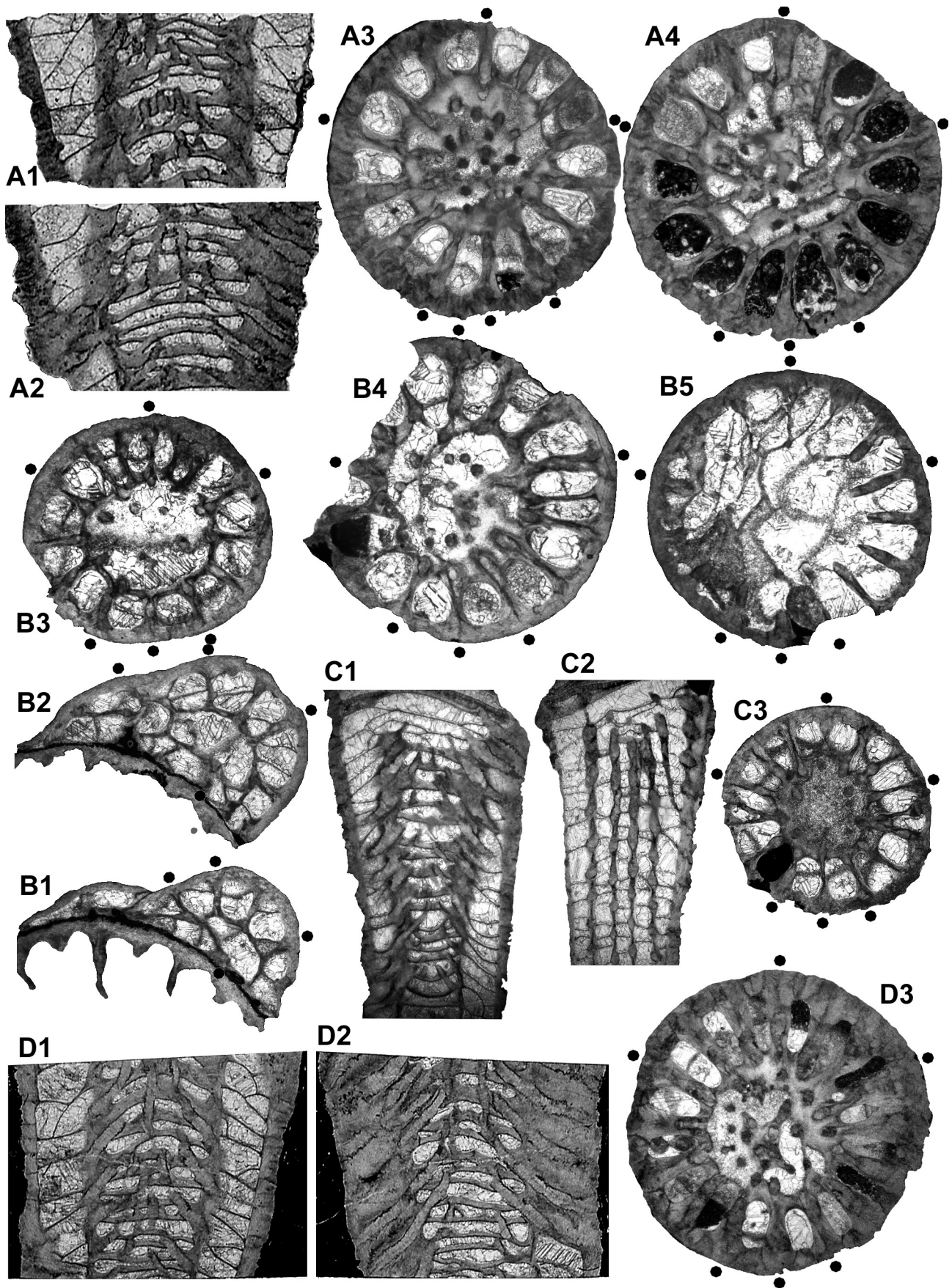
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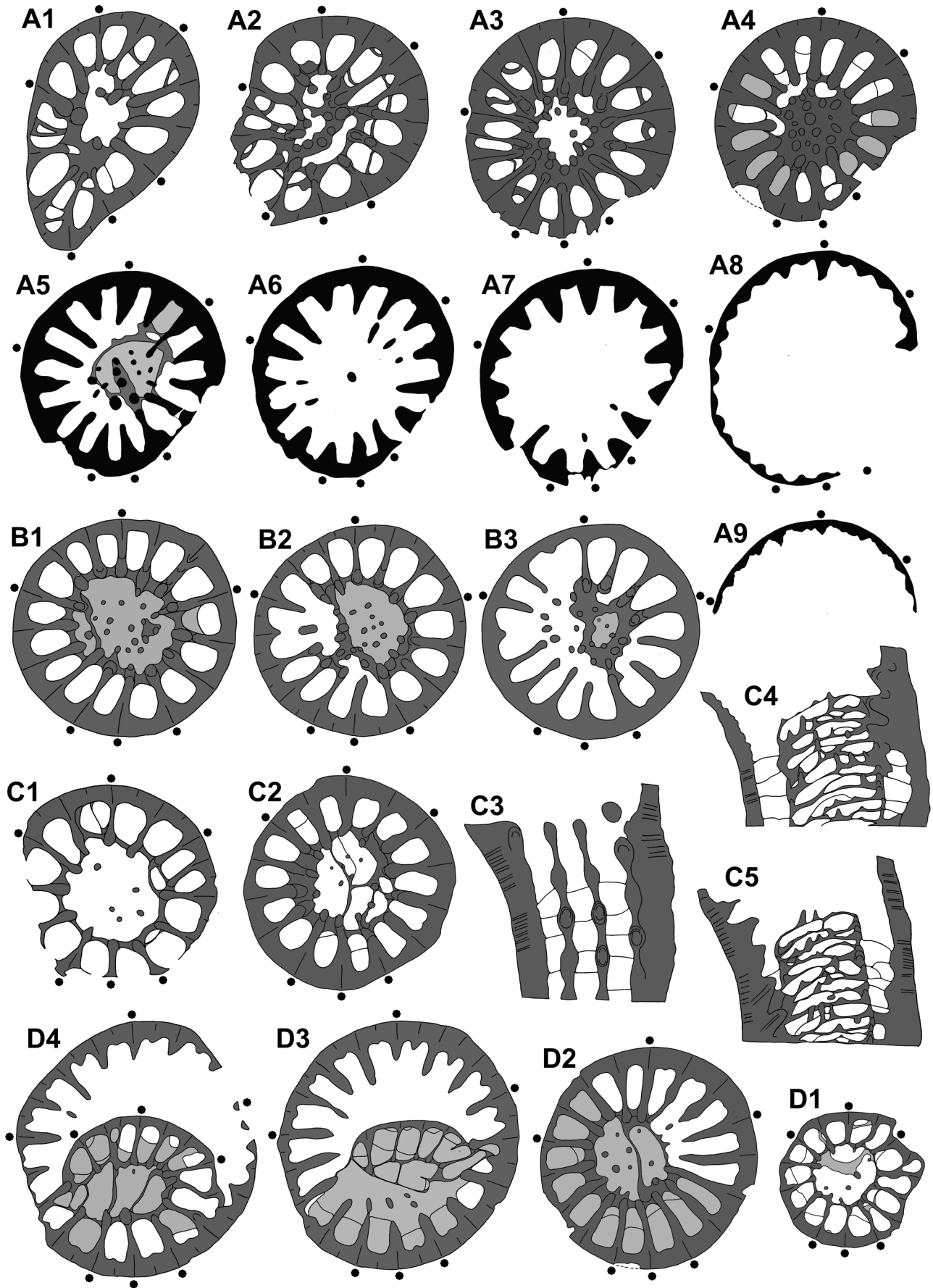
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**Plate 1.** *Spinaxon potyi* sp. nov., holotype and paratypes, Vogelsberg quarry NNE of Göschitz, upper Vogelsberg Formation, Upper Frasnian, probably Lower *Palmatolepis rhenana* Zone, coll. D. Weyer 1983-1984. A1-5. MB.K.7956, bed A, series of cross sections (nos 11, 10, 9, 7 = subtabular, 3 = calicular), x12 (A1), x10 (A2), x8 (A3), and x6 (A4, A5) (drawings see Pl. 3 1-9). B1-3. MB.K.7955, bed B, subtabular sections, x10 (B1), x8 (B2), and x7 (B3). C1-2. MB.K.7963, bed 2, subtabular (C1) and calicular (C2) cross section, x7 (drawing see Fig. 7 B). D1-2. MB.K.7961, bed B, sections (nos 9, 5) near the calicular base, x6 (drawing see Pl. 3 D1-4). E1-2. MB.K.7962, bed 3, median (E1) and slightly eccentric (E2) longitudinal sections (nos 8, 6), x8 (drawings see Pl. 3 C1-5). F. MB.K.7959, bed 3, cross section (no. 2) in the lower calice, x6 (drawings see Pl.3 B1-3). G1-5. MB.K.7957, holotype, bed A, early cross sections (nos 8, 7), x8, and longitudinal sections (nos 5, 2, 1), strongly eccentric outside the circulotheca (G3, G5) and slightly eccentric inside the aulos (G4), x8 (G3) and x7 (G4, G5) (drawings see Fig. 7 A1-4).

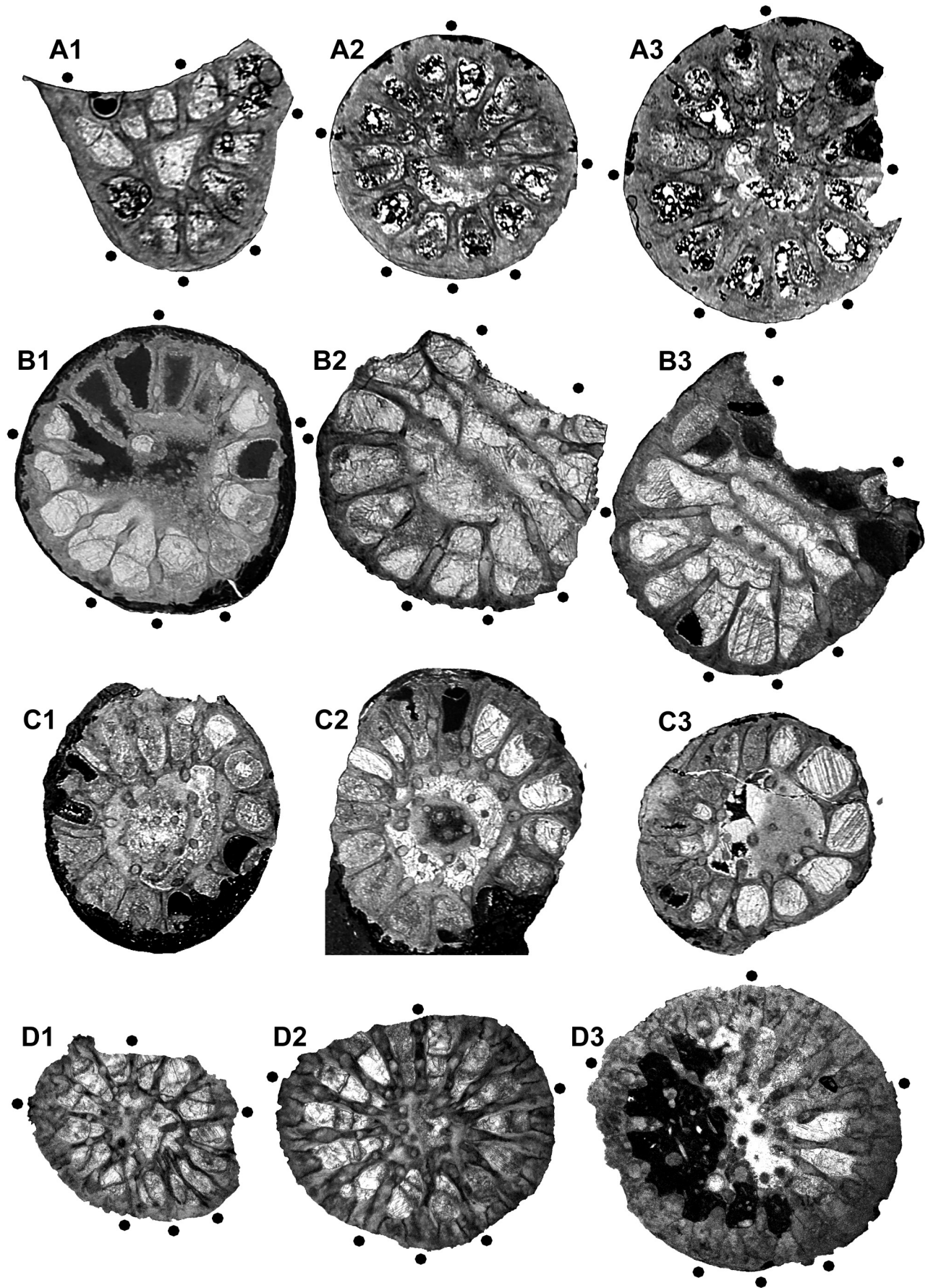


**Plate 2.** *Spinaxon potyi* sp. nov., paratypes, Vogelsberg quarry NNE of Göschitz, upper Vogelsberg Formation, Upper Frasnian, probably Lower *Palmatolepis rhenana* Zone, coll. D. Weyer 1983-1984. A1-4. MB.K.7964, bed AI, slightly eccentric subtabular median longitudinal sections (no. 3a, 3b), x10, and cross sections (nos 4, 5), x8. B1-5. MB.K.7966, bed 3, subtabular cross sections, x10 (B1-4) and x8 (B5, extreme ampleximorph). C1-3. MB.K.7965, bed 2, median and eccentric (outside the aulos) longitudinal section, x6, and basal cross section, x10 (drawing see Fig. 7 C). D1-3. MB.K.7958, bed 1, slightly eccentric and median longitudinal section (nos 6, 7), x7, and cross section (no. 4), x7.



**Plate 3.** *Spinaxon potyi* sp. nov., paratypes, Vogelsberg quarry NNE of Göschitz, upper Vogelsberg Formation, Upper Frasnian, probably Lower *Palmatolepis rhenana* Zone, coll. D. Weyer 1983-1984. A1-9. MB.K.7956, bed A, series of subtabular and calicular cross sections (light grey lumina = calicular in A4, subtabular in A5), x10 (A1-2), x8 (A3), and x6 (A4-9) (photos see Pl. 1 A1-5). B1-3. MB.K.7959, bed 3, cross sections near base of calice (nos 5, 4, 3; lumina calicular at periphery, subtabular within circulotheca), x7 (B1) and x6,5 (B2-3) (photo see Pl. 1 F). C1-5. MB.K.7962, bed 3, subtabular cross sections (nos 9, 7), x10 (C1) and x7 (C2), longitudinal sections with base of calice (C3 tangential outside aulos, x7; C4 slightly eccentric and C5 median within circulotheca, x6) (photos see Pl. 1 E1-2). D1-4. MB.K.7961, bed B, subtabular and basal calicular cross sections with rejuvencence (nos 10, 6, 4, 3, light grey lumina = subtabular), x6 (photos see Pl. 1 D1-2).





**Plate 4.** *Spinaxon potyi* sp. nov., paratypes, Thuringia and Montagne Noire. A1-3. MB.K.7954, upper Coumiac quarry near Cessenon, bed 31b, Lower *Palmatolepis linguiformis* Zone, coll. R. Feist 1992; subtabular and calicular cross sections (nos 6, 4, 3), x15 (A1) and x12 (A2-3) (drawing see Fig. 6 4). B1-3. MB.K.7952, former Kahlleite quarry SW of Rödersdorf, upper Vogelsberg Formation (loose block 14), Upper Frasnian, Lower or Upper *Palmatolepis rhenana* Zone, coll. D. Weyer 1985; subtabular cross sections (nos 5, 2, 1), x10 (B1-2) and x9 (B3) (drawing see Fig. 6 D). C1-3. MB.K.7951, former Kahlleite quarry SW of Rödersdorf, upper Vogelsberg Formation (loose block 13), Upper Frasnian, Upper *Palmatolepis rhenana* Zone, coll. D. Weyer 1985; subtabular cross sections (nos 5, 4, 2), x10 (identification of protosepta impossible). D1-3. MB.K.7960, Vogelsberg quarry NNE of Göschitz, upper Vogelsberg Formation, Upper Frasnian, probably Lower *Palmatolepis rhenana* Zone, coll. D. Weyer 1983-1984, subtabular and basal calicular cross sections, x8 (drawings see Fig. 6 C1-2).