



Neosyringaxon JIA in JIA et al., 1977 (Anthozoa, Rugosa) in the Middle and Late Devonian of Europe and North America

Dieter Weyer and Jean-Claude Rohart

With 4 figures

Abstract: The new species *Neosyringaxon michelini* is described from the lower Frasnian of Ferques near Boulogne-sur-Mer in northern France. The genus (family Petraiiidae) was only known from the lower Givetian of southern China. Further species were found by revision of older literature data: *Zaphrentis polonica* SOBOLÉV, 1904 from the lower Givetian of Skafy, Holy Cross Mountains, Poland (meanwhile assigned to *Stewartophyllum*, *Adradosia*) and *Syringaxon independense* STAINBROOK, 1946 and *Syringaxon calvini* STAINBROOK, 1946, from the Frasnian Independence Shale of Iowa, USA are now transferred to *Neosyringaxon*. Such a disjunctive record occurs often in Cyathaxoniid assemblages of ahermatypic Rugosa and suggests a perhaps nearly cosmopolitan distribution.

Key words: Ahermatypic corals, Givetian–Frasnian, morphology, taxonomy, palaeobiogeography.

1. Introduction

The coral genus *Neosyringaxon* was proposed by JIA (1977) for ahermatypic Givetian Rugosa (family Laccophyllidae) from the Xiangzhou County (around Laibing City, Guangxi Province, southern China). Worldwide, there are no further records from other regions and countries. The originally included three new species seem to be conspecific; they were found in the upper part of the Donggangling Formation (Tunkanling Formation in YOH 1937) “in the vicinity of Xiangzhou County” (*Neosyringaxon elegantum*) and “near Shixianghe reservoir, Xiangzhou County” (*Neosyringaxon guangxiense*, *Neosyringaxon regulare*). JIN & HE (1982: 112, 115) mentioned a more precise lower Givetian age. Two handbooks cited the taxon: HILL (1981: F195) as a questionable synonym of *Syringaxon* LINDSTRÖM, 1882 (Laccophyllinae GRABAU, 1928), surely an erroneous classification as there are no contrasting minor septa; LIN et al. (1995, p. 393) changed correctly the subfamily position to Neaxo-

ninae HILL, 1981, which are now a junior synonym of Petraiiidae KONINCK, 1872 (WEYER 2000: 78).

Unexpectedly, we found a new species *Neosyringaxon michelini* among our collections of lower Frasnian corals from France. Critical research in older publications demonstrates the additional presence of the genus in Poland (lower Givetian, Holy Cross Mountains) and even in North America (Frasnian, Iowa, USA). This curious disjunctive distributional pattern cannot surprise; it reflects only the present poor knowledge about such small dysphotoc/aphotic coldwater, often cosmopolitan Rugosa (with a special research deficit in the Givetian and in the Frasnian).

2. Ahermatypic Rugosa in the Boulonnais, northern France

Lower–middle Frasnian dysphotoc/aphotic coldwater corals from Ferques near Boulogne-sur-Mer were

first described by MICHELIN (1845: 183, pl. 47, fig. 7) as “*Cyathophyllum mitratum* (SCHLOTHEIM, 1820)”, which is quite another taxon from the Silurian of Gotland (type species of *Pycnactis* RYDER, 1926, with lectotype designation by LANG & SMITH 1927: 471).

MILNE-EDWARDS & HAIME (1850: LXIX, 1851: 318) proposed a new genus for this coral from Ferques and renamed it *Metriophyllum bouchardi* MILNE-EDWARDS & HAIME, 1850 (later becoming the type of the family Metriophyllidae HILL, 1939, and of the suborder Metriophyllina SPASSKIY, 1965). This was done using excellently preserved specimens with a free-weathered calice, but still before the introduction of thin section techniques for the study of Palaeozoic Rugosa, which started in Germany with KUNTH (1869a). The necessary lectotype designation was published by LANG *et al.* (1940: 84): the coral figured in pl. 7, fig. 1, 1a of MILNE-EDWARDS & HAIME (1851), Devonian, Ferques near Boulogne (copied in STUMM 1949: pl. 3, figs. 1, 2). This lectotype specimen is lost in the MILNE-EDWARDS collection of the Musée National d’Histoire Naturelle in Paris (HOLWILL 1964: 112; information 2019 of Dr. SYLVAIN CHARBONNIER and Dr. JEAN-MICHEL PACAUD, Paris).

A first revision including topotypes was published by BARROS (1882: 196). His improved diagnosis of *Metriophyllum* showed the typical septal flanges (later called metriophylloid carinae) and the absence of a pseudocolumella; it was accepted by SCHLÜTER (1889), GLINSKI (1963), FEDOROWSKI (1965), PEDDER (1967), and others. Current views on the taxonomy of *Metriophyllum* (HILL 1981: F190) suffer from inadequate revisions based on wrong “topotypes” (SMITH 1945; HOLWILL 1964; WEYER 1970; SCRUTTON 1985), which are not congeneric with the lectotype illustration. These authors were not aware of the existence of two different, quite homoeomorphic genera in the local Frasnian (in different stratigraphic levels); and they incorrectly referred to the morphology without antiseptal triad, not identical with the lost lectotype of *Metriophyllum bouchardi* MILNE-EDWARDS & HAIME, 1850. Better stratified new collections enable us (ROHART & WEYER 2020) to propose a neotype for the *Metriophyllum* type species: main diagnostic features are the trabecular septal microstructure, and the triad formed by the antiseptum and its two neighbouring long minor septa; all other minor septa are short and become reduced during the calicular ontogenesis (then being hidden within the archaeotheca). The older “*Metriophyllum-II*” has no such triad and will be revised as a separate new species in a future publication.

The presence of two different “Metriophyllids” near Ferques was already mentioned in WEYER (1991: 11) and WEYER (1996: 86).

“*Metriophyllum-I*” (middle Frasnian Ferques Formation) – with cardinal fossula (cardinal septum shortened) and long counter minor septa forming an antiseptal triad, without aulos. Synonyms are *Lindstroemia* NICHOLSON & THOMSON, 1876 and *Lopholasma* SIMPSON, 1900. Without any doubts, this is the true genus *Metriophyllum*, when compared with the calicular view of the lectotype illustration (MILNE-EDWARDS & HAIME 1851, pl. 7, fig. 1a), which offers a clear morphological picture of the septal apparatus, with 44 septa (22 of them traditionally accepted as major septa, but in reality 26 major septa, if the last “minor septum” at every of the four insertion points is accepted as a morphogenetical major septum). The 1851 drawing of the lectotype calice seems remarkably exact in view of the details in the “north” of the figure: counter septum with two neighbouring contratingent, very long counter minor septa, forming together a distinct triad; all other minor septa being free and very short. This reflects correct observation and objective illustration of symmetry facts and construction laws still not fully known to MILNE-EDWARDS & HAIME 1851, later (since LUDWIG 1862; LUDWIG 1865; KUNTH 1869b; SARDESON 1897; FAUROT 1909) described as the “law of KUNTH” ruling the growth of the septal apparatus in Rugosa corals (named LUDWIG/KUNTH-law by WEYER 2008). Already CARRUTHERS (1913: 50) stated that the figures “given by MILNE-EDWARDS & HAIME are remarkably faithful” (an opinion achieved after his investigations of their collections in Paris, 1907).

“*Metriophyllum-II*” (lower Frasnian Beaulieu Formation) – with aulos, without antiseptal triad and fossula. Nearly all hitherto published “topotypic” cross sections of *Metriophyllum bouchardi* (perhaps except SMITH 1945: pl. 1, figs. 12, 13, but including those copied in HILL 1981: fig. 113.2a, b) belong to this group, but are a misinterpretation of the real type species.

These results lead to some radical changes in nomenclature (WEYER 1996: 85). The suborder Metriophyllina SPASSKIY, 1965 now becomes a senior synonym of Stereolasmatina HILL, 1981, but both are to be replaced by the still senior synonym Zaphrentoidina WANG, 1950 (again proposed as new by SCHOUPPE & STACUL 1959). WANG (1950: 203) did not mention any authorship for suborders and families, but later (WANG & CHEN 1989a: 187; WANG & CHEN 1989b: 52) he attributed the authorship of the suborder Zaphrentoidina to SCHINDEWOLF (1938). This was not correct,

because SCHINDEWOLF (1938: 451, 452) had proposed only a new family name Zaphrentoididae, which at that time was unnecessary because of the already existing Hapsiphyllidae GRABAU, 1928 (rejected by SCHINDEWOLF against the rules of zoological nomenclature ICZN 1905, because he had classified *Hapsiphyllum* SIMPSON, 1900 only as a subgenus of *Zaphrentoides* STUCKENBERG, 1895). The family taxon Metriophyllidae HILL, 1939 is now a senior synonym of Stereolasmatidae FOMICHEV, 1953, but a junior synonym of Lindstroemiidae POČTA, 1902. Also the „Metriophyllina“ sensu HILL (1981: F186) must be renamed – the taxon *Cyathaxoniina* SPASSKIY, 1977 is available (SPASSKIY 1977: 25, 153); here, „*Metriophyllum*-II“ will be a member of probably *Petraiidae* KONINCK, 1872. Metriophylloid carinae are a feature, which had arisen during Silurian– Permian times independently in several suborders and in many families of Rugosa (as suggested by PEDDER 1967: 110, and underlined by FEDOROWSKI 1986).

ROHART (1988, 2002, in BRICE et al. 2002, in MISTAEN et al. 2002) recorded further ahermatypic Rugosa (besides of the traditional *Metriophyllum*) and indicated their different stratigraphic positions within the Frasnian of the Boulonnais: *Metrioplexus richerti* GLINSKI, 1963, *Metrioplexus* cf. *carinatus* RÓZKOWSKA, 1969, *Catactotoechus? variabilis* ROHART, 1988 (Fig. 1). Surprisingly, our “*Metriophyllum*” collections contain a rare fifth genus, hitherto not described from the Frasnian of Europe; the unique specimen is to classify within *Neosyringaxon* JIA in JIA et al., 1977. Today, intensive serial sectioning is indispensable for modern investigations of such small, externally similar and indistinguishable, but diverse coral communities, and often several historical determinations (MICHELIN 1845, MILNE-EDWARDS & HAIME 1851: pl. 7, fig. 2, paralectotype *Metriophyllum bouchardi*) cannot be revised after the loss of old collections.

The base of our revisions was the highly improved actual knowledge about the stratigraphy of the Middle–Upper Devonian from Ferques (Boulonnais), as started by RIGAUX (1892, 1908) and recently elaborated in BRICE (1988): a modern detailed lithostratigraphy of the ca. 250 m thick lower– middle Frasnian sequence (Beaulieu and Ferques Formations, sometimes yielding corals), precisely stratified new collections, nearly monographic faunal/microfloral studies. Historical fossil samples, distributed in many European museums and usually labelled only “Ferques” (without exact locality data) and simply “middle Devonian” or “upper Devonian”, now have lost their ancient

value and are better not used as real topotypes, as done in the unsuccessful case of *Metriophyllum bouchardi* (MILNE-EDWARDS & HAIME, 1850). Our new materials of Frasnian ahermatypic corals come from eight different localities (Fig. 2).

Corals like this *Metriophyllum/Catactotoechus/Neosyringaxon* assemblage from Ferques (Boulonnais) belong to an ecological group of Rugosa, termed by HILL (1938: 5) as *Cyathaxonia* fauna. Such communities (dysphotic/aphotic, ahermatypic, coldwater, basinal, cephalopod facies) are distributed in upper Silurian– Permian times; they seem to start rarely in the Wenlockian and appear widespread in the Ludlowian. Earlier records during the upper Ordovician and lower Silurian are problematic (especially the presumed age of *Protozaphrentis* YU, 1957). When dealing with Devonian faunas, OLIVER (1992: 139) preferred the term laccophyllid assemblage, because *Cyathaxonia* MICHELIN, 1847 was seen as a Carboniferous coral (in spite of RÓZKOWSKA 1969, who found the genus throughout the Famennian). The direct ancestor of *Cyathaxonia* is *Laccophyllum* SIMPSON, 1900 (WEYER 1994: 183); both genera are classified by HILL (1981) into two separate families Laccophyllidae GRABAU, 1928 and *Cyathaxoniidae* MILNE-EDWARDS & HAIME, 1850 of the suborder Metriophyllina SPASSKIY, 1965. The phylogenetic radiation would not require such a high rank within the family group. The lower tribus level might be enough – Laccophyllini and *Cyathaxoniini*, even when an enlarged future phylogenetic row might be accepted: *Laccophyllum*-I (trabicular septal microstructure, perhaps mainly Silurian–Devonian)→*Laccophyllum*-II (fibro-normal septal microstructure, perhaps mainly lower Carboniferous)→*Cyathaxonia*, which implies the mostly accepted synonymy of *Cyathocarinia* SOSHKINA, 1928, as smooth or granulated septal flanks can be valued only as specific criteria. The latter feature also occurs in the ancestral genus *Laccophyllum*: Famennian specimens with spiny septal flanks described by GORSKIY (1932) and in the WEYER collections. The name *Cyathaxoniid*-assemblages (like HILL 1938) seems appropriate; in the Silurian they are composed by taxa of the suborders *Cyathaxoniina* SPASSKIY, 1977 and *Plerophyllina* SOKOLOV, 1960, and in the Devonian–Permian an additional third suborder *Zaphrentoidina* WANG, 1950 appears.

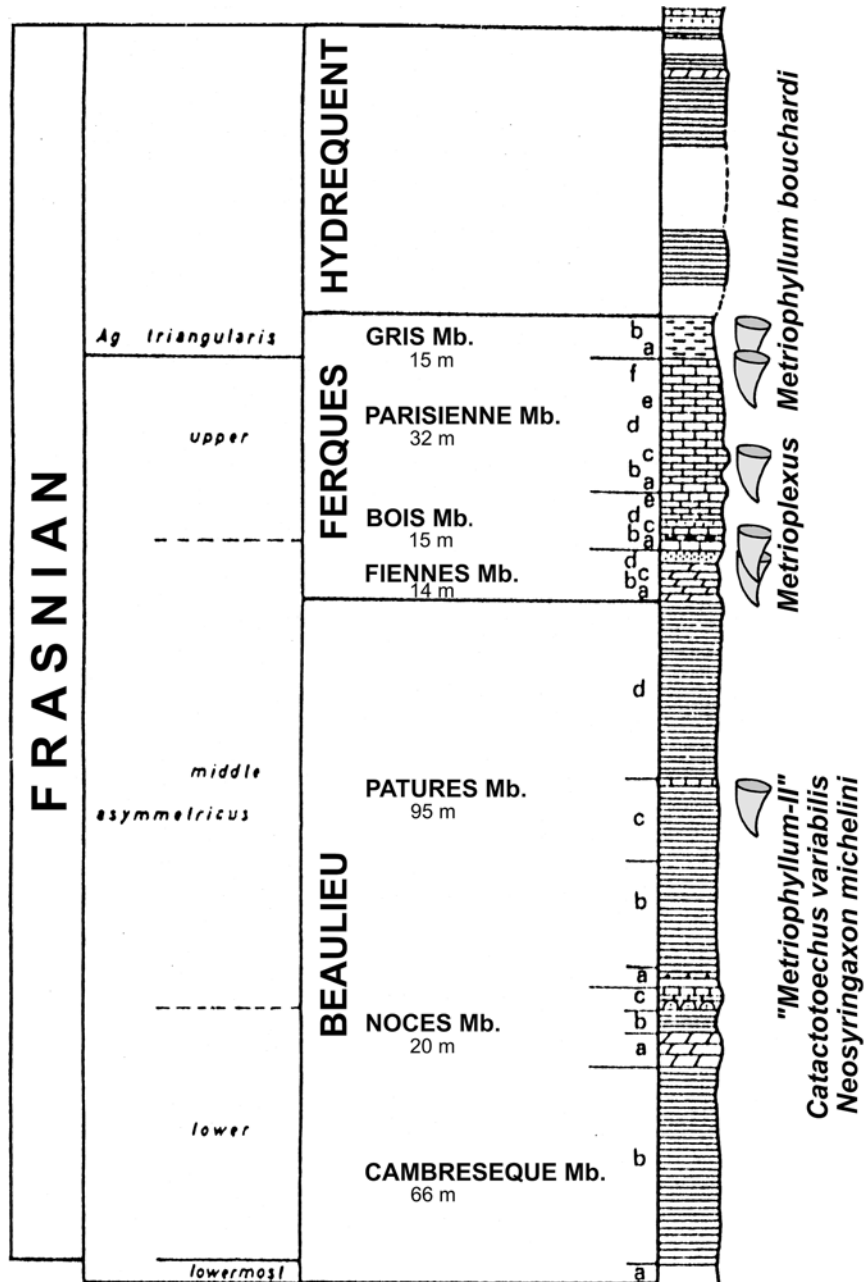


Fig. 1. Distribution of ahermatypic Rugosa in the lower–middle Frasnian sequence of Ferques, Boulonnais (lithostratigraphy and conodont zonation after BRICE 1988, BRICE et al. 2002; coral data after ROHART 1988, ROHART 2002, and MISTIAEN et al. 2002).

3. *Neosyringaxon* in the Holy Cross Mountains (Poland) and in Iowa (USA)

The ahermatypic Rugosa community of the lower Givetian brachiopod shales from the famous locality Skąły include the species *Zaphrentis polonica* SOBOLEV, 1904, redescribed by FEDOROWSKI

(1965: 344) as *Stewartophyllum polonicum* (SOBOLEV, 1904). WEYER (1985: 20, though with a question mark) and FEDOROWSKI (2003: 61) transferred the species to *Adradosia* BIRENHEIDE & SOTO, 1977, but the juvenile “aulos” (FEDOROWSKI 1965: text-fig. 1D, pl. 3, fig. 3), a circolotheca (sensu FEDOROWSKI 2009: 238), is untypical for such Hapsiphyllidae. The morphology

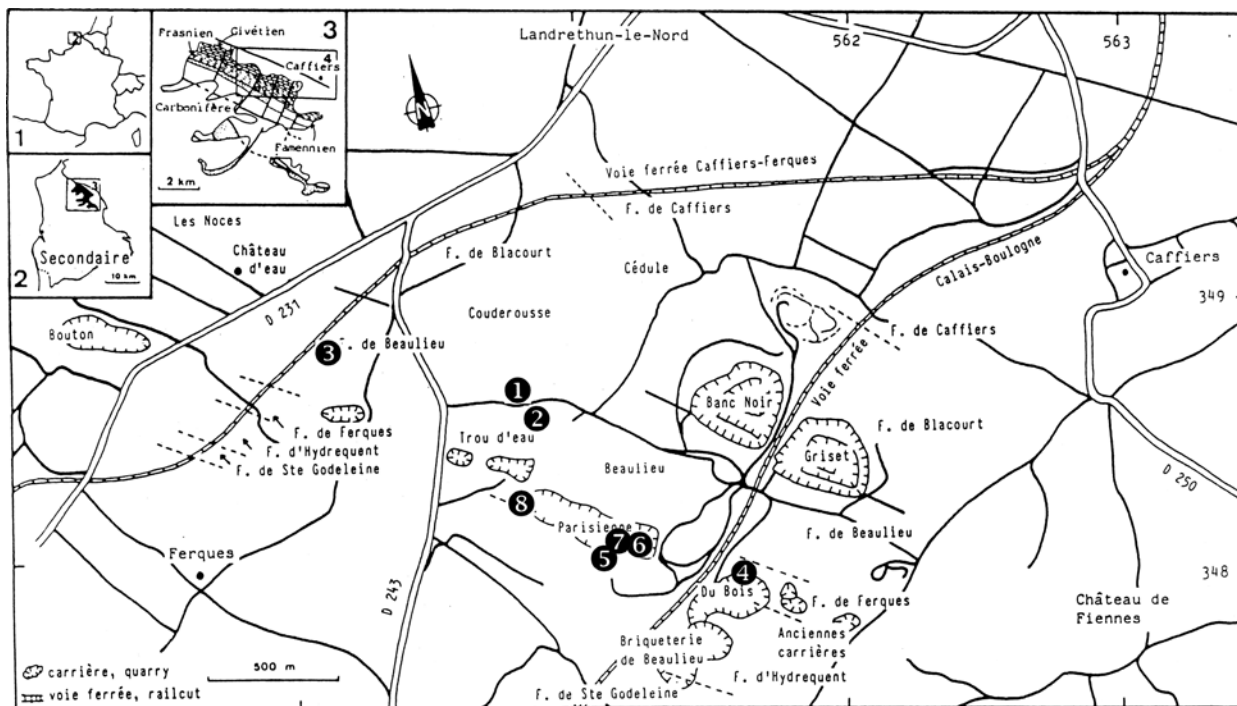


Fig. 2. Localities of lower– middle Frasnian ahermatypic corals near Ferques (Boulonnais, northern France; map after BRICE 1988). **A** – Beaulieu Formation (lower Frasnian). 1. Side road ENE Ferques, leading to the Banc Noir and Griset quarries, outcrop on the northern berm of the first bend. – Pâtures Member, top of the term c. 2. Surface outcrop south of the side road ENE Ferques, leading to the Banc Noir and Griset quarries. – Pâtures Member, term c. 3. Trench of the railway track Caffiers–Ferques. – Pâtures Member, top of the term c. **B** – Ferques Formation (middle Frasnian). 4. Bois de Beaulieu quarry. – Bois Member, term a. 5. La Parisienne quarry, southern slope. – Parisienne Member, term f. 6. La Parisienne quarry, islet at the eastern entrance. – Parisienne Member, term f. 7. La Parisienne quarry, islet at the eastern entrance (above the former). – Gris Member, term a, b. 8. La Parisienne quarry, western face. – Gris Member, term a, b.

seems nearest to *Neosyringaxon* (perhaps except the rather early appearance of the cardinal fossula). The former generic attribution to *Stewartophyllum* BUSCH, 1941 was doubtful; this taxon from the upper Hamilton Group of New York State with its much flatter, even weakly evert(?) calice is insufficiently known (in spite of BUSCH 1941 and STUMM & WATKINS 1961). The latter authors synonymized three new *Barrandephyllum* and *Hapsiphyllum* species of BUSCH (1941) with *Stewartophyllum intermittens* (HALL, 1877), however, without any argumentation.

Syringaxon independense STAINBROOK, 1946 and *Syringaxon calvini* STAINBROOK, 1946 from the Independence Shale (Frasnian) of Independence and Brandon (Iowa, USA) must be excluded from *Syringaxon* LINDSRÖM, 1882 (according to present interpretations, following SUTHERLAND 1970) – their minor septa are short and not contratingent, and their cardinal septum is shortened. The morphology (rather well described

in 1946) corresponds to *Neosyringaxon*; available data seem sufficient for such a reclassification, though today more intensive studied ontogenetic facts (from basal tip to upper calice) are desired.

4. Systematic palaeontology

- Class Anthozoa EHRENBERG, 1834
- Subclass Zoantharia BLAINVILLE, 1830
- Superorder Rugosa MILNE-EDWARDS & HAIME, 1850
- Order Stauriida VERRILL, 1865
- Suborder Cyathaxoniina SPASSKIY, 1977

Family Petraiidae KONINCK, 1872

Synonym: Neaxoninae HILL, 1981.

Remarks: The traditional concept of this family (HILL 1981: F187) was criticized by WEYER (1978b: 100, 1980), refusing the generally accepted “*Petraia* revision” of SCHINDEWOLF (1931), who had violated the International Code of Zoological Nomenclature (from 1st edition, ICZN 1905, valid in the times of SCHINDEWOLF, up to the actual 4th edition, ICZN 1999) by a severe manipulation of the type species. The necessary revision of *Petraia decussata* MÜNSTER, 1839, the real type species (upper Famennian) designated by MILLER (1889: 199), was published rather late (WEYER 2000: 80); it caused a drastic change in the definition of the family Petraiididae (now a senior synonym of Neaxoninae HILL, 1981, due to the postulated phylogenetic line *Neaxon*→*Petraia*). SCHINDEWOLF (1931) used the Silurian *Petraia radiata* MÜNSTER, 1839 as type species, however defined it not by its lectotype (MÜNSTER collection, Ludlow), which is a species of *Palaeocyathus* FOERSTE, 1888 (Enterolasmatinae HILL, 1981), but by his own specimen collected in 1922 and of course better prepared by thin sections, now revised as *Muenstraia franconica* WEYER, 2001 (Ludlow, Protozaphrentidae IVANOVSKIY, 1959). The new interpretation of the family Petraiididae was discussed by letter in 1987 with JERZY FEDOROWSKI, who then already used this concept (FEDOROWSKI & SANDO 1989; FEDOROWSKI 1990).

Included genera: *Petraia* MÜNSTER, 1839, *Trochophyllum* MILNE-EDWARDS & HAIME, 1850, *Meniscophyllum* SIMPSON, 1900, *Nicholsoniella* SOSHKINA, 1952, *Catactotoechus* HILL, 1954, *Neaxon* KULLMANN, 1965, *Czarnockia* RÓZKOWSKA, 1969, *Hillaxon* RÓZKOWSKA, 1969, *Neosyringaxon* JIA in JIA et al., 1977, *Neaxonella* WEYER, 1978a, *Accurganax* LI, 1979 (?Synonym *Marocaxon* BERKOWSKI 2008), *Paliaxon* WEYER, 1981, *Patularima* FEDOROWSKI, 1990, *Erfoudia* BERKOWSKI 2008, *Spinaxon* WEYER 2016.

For the moment, necessary subfamilies and tribes are not used – the phylogenetic relationships during stratigraphic times remain ambiguous. A separation of all pleonophorous taxa would result in a polyphyletic classification, as dissepiments developed repeatedly in independent groups and can not be judged automatically as a criterion of the family group. Some provisional phyletic lines as *Neaxon*→*Petraia*→*Famennelasma*→*Czarnockia* and *Neaxon*→*Neosyringaxon*→*Nicholsoniella* were proposed (WEYER 2000: 82, 89), but they are incomplete and not stratigraphically controlled. Extinction (e.g., *Neaxon*) and survival during the global Hangenberg Event (Devonian– Carboniferous boundary) are not finally explored. Often further genera as *Guerichiphyllum* RÓZKOWSKA, 1969 (a polyphyletic Givetian–Famennian assemblage), *Nalivkinella* SOSHKINA, 1939, *Gorizdronia* RÓZKOWSKA, 1969, *Famennelasma* WEYER, 1973 (? synonym of *Friedbergia* RÓZKOWSKA, 1969), *Hebukophyllum* LIAO & CAI, 1987, *Circellia* YE & WANG, 1983 (and the available subfamily names *Friedbergiinae* RÓZKOWSKA, 1969, *Guerichiphyllinae* RÓZKOWSKA, 1969) had been related to the *Neaxon* group – in part, but not always correctly.

Genus *Neosyringaxon* JIA in JIA et al., 1977

1977 *Neosyringaxon* gen. nov. – JIA in JIA et al., p. 118.
?1978 *Neaxonella* n. gen. – WEYER, p. 292.

Type species (original designation): *Neosyringaxon elegantum* JIA in JIA et al., 1977, Givetian of Xiangzhou County, Guangxi Province, southern China (lower Givetian according to JIN & HE 1982: 112, 115). JIA (1977) described three rather well-illustrated species. The short original descriptions are cited below in the English translation of JIA HUI-ZHEN. Her photographs of the subtabular and calicular transverse sections are extremely similar and allow the suggestion that they represent only one species; it should be verified that they come from one “population”.

Neosyringaxon elegantum JIA in JIA et al. 1977, p. 119, pl. 41, fig. 2a–e.

Conical solitary corals, diameter 13–15 mm, length 38 mm. External wall (as seen in transverse sections) formed by broadened septal bases; its mature average thickness is 1.4–1.6 mm. Major septa long in early stages and meeting in the centre. Mature major septa (number 24) reach a length of $\frac{3}{4}$ radius. Minor septa short. Size of “columella” [= circulotheca] in average $\frac{1}{2}$ corallum diameter. Tabulae are steeply domed from the external wall against the circulotheca. Distance of tabulae ca. 0.5–1.0 mm. No dissepiments.

Neosyringaxon guangxiense JIA in JIA et al., 1977, p. 119, pl. 41, fig. 3a, b.

Diameter 11–12 mm. Width of peripheral stereozone 0.8 mm. Width of aulos 1.2–2.5 mm. 26 major septa; their length is $\frac{4}{5}$ radius. No minor septa. Tabulae are steeply domed from the external wall against the circulotheca. Distance of tabulae 0.5–0.7 mm. No dissepiments.

Neosyringaxon regulare JIA in JIA et al., 1977, p. 119, pl. 41, fig. 5a–d.

Diameter 11–12 mm. Width of peripheral stereozone 0.9 mm. Diameter of oval aulos 1–3 mm. 24 major septa; their length at maturity $\frac{2}{3}$ – $\frac{4}{5}$ radius. No minor septa. Tabulae are steeply domed from the external wall against the circulotheca. Distance of tabulae 1.4–1.6 mm. No dissepiments.

Original diagnosis (English translation, sent by JIA HUI-ZHEN to RUDOLF BIRENHEIDE): “Small, simple, conical corals. All septa dilate peripherally to form a wide peripheral stereozone. Major septa are thick. In brevic stage they extend to axis and form a stereocolumella. In neanic and ephebic stages their axial ends retreat from the axis to form an elliptical aulos which is filled up by lime carbonate to form a firm stereocolumella. In the late ephebic stage the aulos becomes hollow, and a cardinal septum retreats from the axis to form a horseshoe-shaped inner wall and a cardinal fossula. Minor septa are very short. Tabulae slope upwards from the epitheca to the axis. No dissepiments. This genus is marked by three developed stages: an early *Stereolasma* (brephebic) stage, *Syringaxon* (neanic) stage, and *Hapsiphyllum* (ephebic) stage.

Discussion: This genus is similar to such as *Stereolasma*, *Syringaxon* and *Hapsiphyllum*. It differs from the first and second in that the stereocolumella is composed of an aulos filled with lime carbonate; from the third in that there are stereocolumella in the brephebic, neanic and ephebic stages. *Lophophyllidium* differs from the new genus in its columella derived from the thickened axial end of the counter septum.”

Type species: *Neosyringaxon elegantum* JIA in JIA et al., 1977.

Distribution and age: Late Middle Devonian of Kwangsi Province, China.

Emended diagnosis: Small diaphragmatophorous conical corals, in the youth like *Neaxon* with radial arranged major septa forming axially a complete circulotheca, at maturity with shortened cardinal septum in a fossula interrupting the aulos. Minor septa active only in the upper calice, reduced and incorporated into the thickening archaeotheca during middle/lower calicular phases. Septal microstructure tabular. Tabulae highly domed.

Comparisons: The ancestral genus *Neaxon* KULLMANN, 1965 differs in its never shortened cardinal septum and in its always persistent cyclotheca, both typical plesiomorph features. Another *Neaxon* descendant, *Petraia* MÜNSTER, 1839, is similar in the shortening of the cardinal septum, but differs in its loss of the cyclotheca, which becomes disconnected everywhere in all four quadrants (not only at the cardinal fossula). The *Neosyringaxon* descendant *Nicholsoniella* SOSHKINA, 1952 with quite comparable growth stages (WEYER 2000, text-fig. 2.3, pl. 6, fig. 1a) acquires a small dissepimental zone in the mature calice.

The early Upper Emsian genus *Neaxonella* WEYER, 1978 was proposed nearly simultaneously, not yet knowing the Chinese Atlas of JIA et al. (1977); at first glance it looks like a junior synonym of *Neosyringaxon*. But the older taxon differs in two already apomorph features connected with the minor septa: the short and free catasepta (at first reduced during lower calicular ontogenetic phases) persist active at the mature calicular base, and there a first trend towards a biform tabularium appears. This might justify a separate genus, but at present such morphologies are so poorly known (or even unknown) in late Upper Emsian and Eiflian times, that any decision about synonymy (yes or not) would be premature.

Assigned species: *Neosyringaxon elegantum* JIA in JIA et al., 1977 (synonyms: *Neosyringaxon guangxiense* JIA in JIA et al., 1977; *Neosyringaxon regulare* JIA in JIA et al., 1977). – Givetian, China.

Neosyringaxon polonicum (SOBOLEV, 1904) – Givetian, Poland.

Neosyringaxon calvini (STAINBROOK, 1946) – Frasnian, USA.

Neosyringaxon independense (STAINBROOK, 1946) – Frasnian, USA.

Neosyringaxon michelini sp. nov. – Frasnian, France.

A much larger regional distribution in many further countries is expected, where such ahermatypic Rugosa remained undescribed/unrevised and even uncollected up to date.

Neosyringaxon michelini n. sp.

Figs. 3A–G, 4A–Q

Etymology: After JEAN-LOUIS HARDOUIN MICHELIN (1786–1867), who described the first Devonian corals from the Boulonnais region in northern France.

Holotype: The for the moment only available specimen no. MNHN.F.A71230 (collection J.-C. ROHART ca. 1975), Musée Nationale d'Histoire Naturelle, Paris – 15 transverse sections (11 peels, 4 thin sections), 1 remaining piece.

Type locality: Side road ENE of Ferques, leading to the Banc Noir and Le Griset quarries (and to the Beaulieu wood), outcrop on the northern slope at the first bend (locality 1 in Fig. 2).

Type horizon: Beaulieu Formation, Pâtures Member, top of level c (RIGAUX 1892: Calcaire à *Pentamerus* supérieur = *Metabolipa meatsi* BRICE, 1988; BRICE et al. 1976: 136, fig. 1, tab. 1; BRICE et al. 1979: 316, fig. 3). *Disphyllum gradatum* (TSIEN, 1970) and *Catactotoechus? variabilis* ROHART, 1988 were described by ROHART (1988: 235, 240, 256) from this locality; also “*Metriophyllum-II*” occurs. In 1993, we both recollected the same taxa.

Diagnosis: Small species of *Neosyringaxon* with 38 septa (23 major septa) at 7.4 mm diameter, minor septa active only at uppermost calicular rim. Width of mature cyclotheca 20% of diameter. Well shortened cardinal septum growing longer only at base of triangular fossula interrupting the aulos.

Description: The only available holotype is a small conical, slightly cornute corallum (length 12 mm, diameter of broken tip 1.5 mm, distal diameter of incompletely preserved upper calice 7.4 mm, cardinal septum at concave side). The archaeotheca bears growth rugae and longitudinal furrows of major and minor septa (according to the bifurcating furrows and the intercalated ribs – schizosepta in the sense of WEYER 2008: 108; no hyposeptal furrows); there occurs an overgrowing small auloporiid Tabulata colony.

The calice occupies half of the length; originally it was distinctly more, as an upper calicular portion is abraded. The highest available transverse section (Fig. 4O) presents seemingly 20 major septa, in reality there are 23 (the last one of the cardinal quadrants and of the left counter quadrant as usual still imitating minor septa, here situated secondarily reduced hidden within the thickened wall – adult 6 protosepta, 17 metasepta, 15 catasepta). The major septa are radially arranged and nearly of equal length except the strongly shortened cardinal septum; they are never thin as a thread, but start broad-based at the wall and thinning continuously towards the centre. The two penultimate cardinal metasepta are slightly shorter (in order to surround the triangular cardinal fossula deeper in the calice). There no longer appear any minor septa protruding into the lumen, but locally it is indicated that they were active a little higher in the not preserved uppermost calice (nearly invisible slight protuberances in the right cardinal quadrant, different interior wall thickening in positions I and II in the sense of SUTHERLAND 1965). Their general primary presence (as typical for every Rugosa, here following the Stauriida-model with antiseptal minor septa) during all growth stages is shown by the corresponding external furrows of the archaeotheca (Fig. 4A, E, F, L, N).

The sequence of further calicular transverse sections (Fig. 4I–N) demonstrates the primary calicular ontogeny of skeletal growth resulting in the morphological view of the basal calice (Fig. 4H), which alone is shown in all earlier subtabular sections. Major septa prolongate (though never

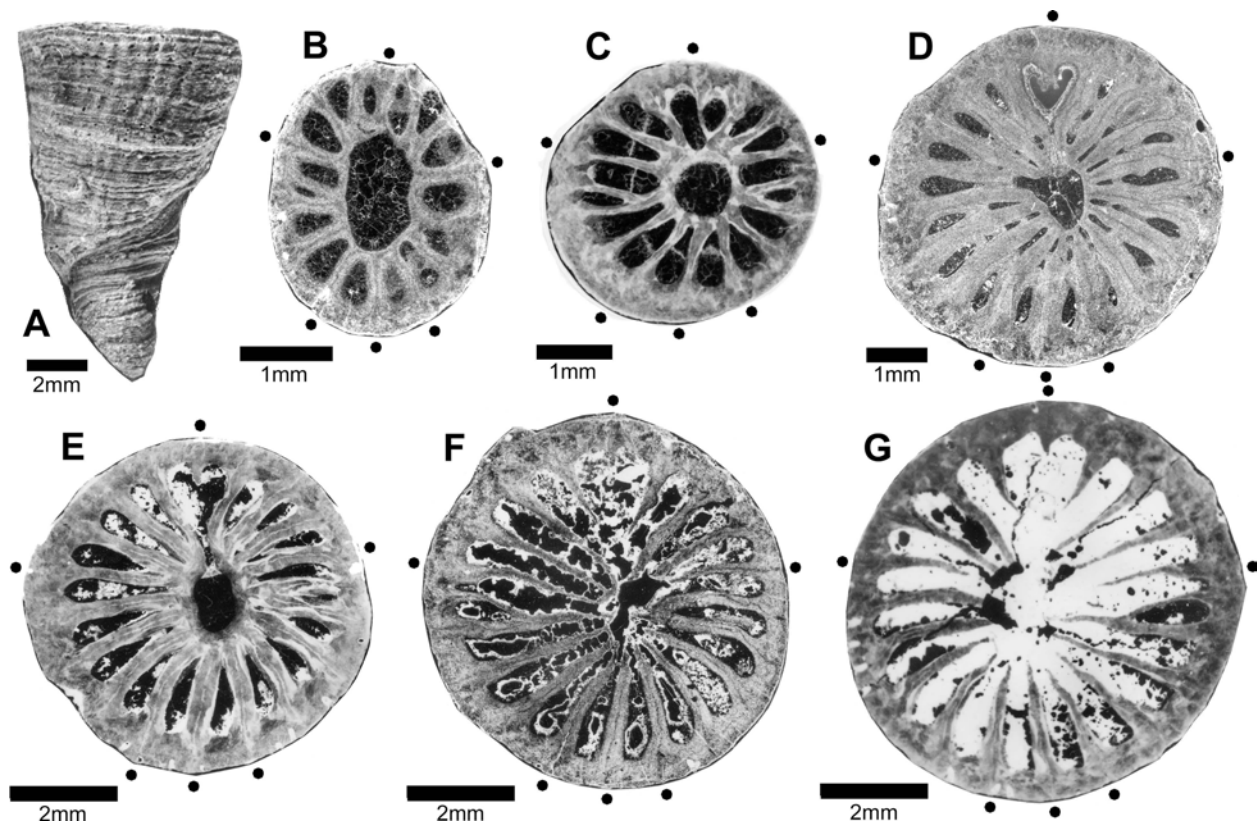


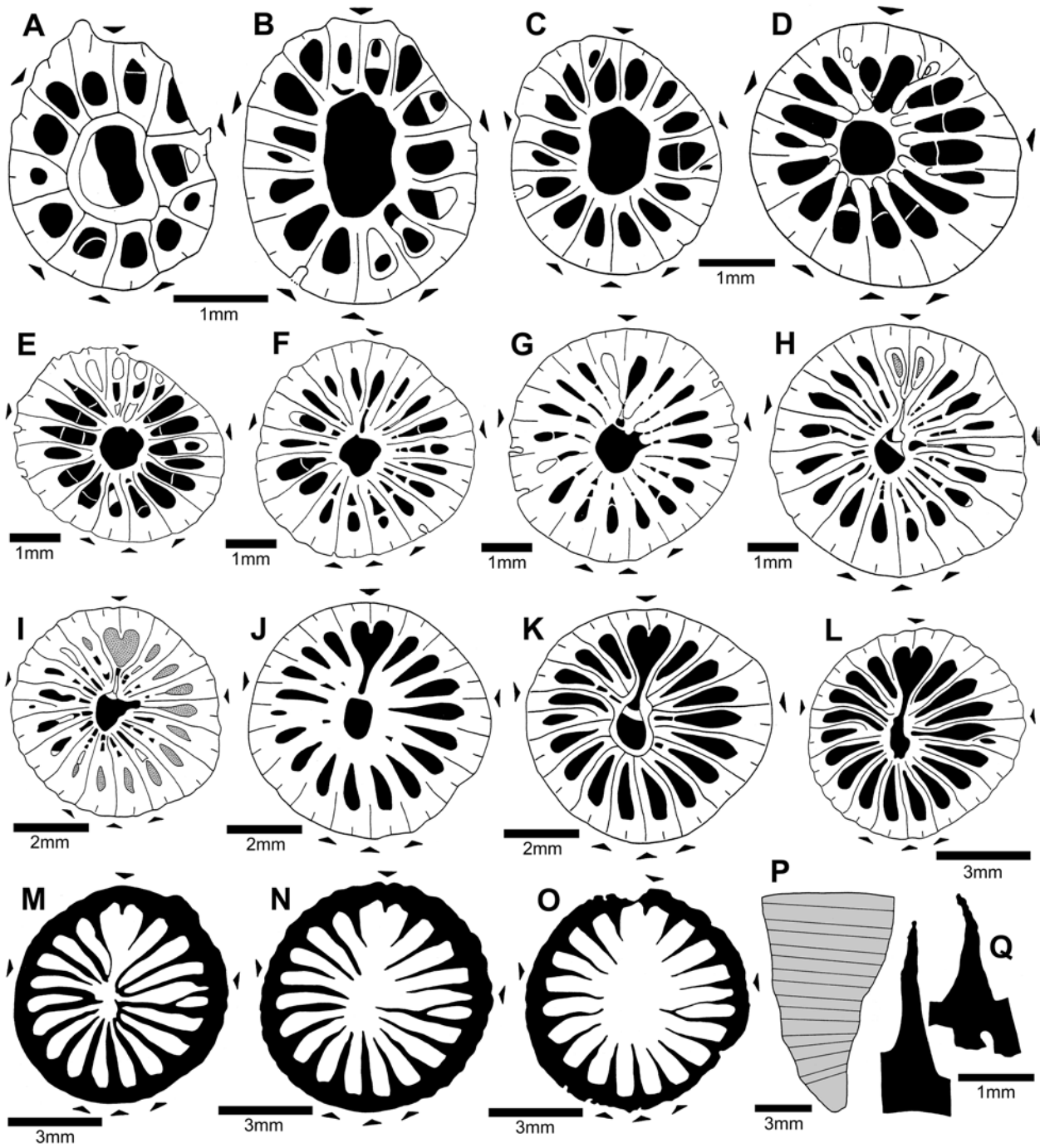
Fig. 3. *Neosyringaxon michelini* sp. n., holotype no. MNHN.F.A71230 (Paris), lower Frasnian (Pâtures Member of Beaulieu Formation, top of level c), side road ENE Ferques (leading to the Banc Noir and Le Grisset quarries), collection J.-C. ROHART ca. 1975. **A** – Lateral view of slightly cornute corallum. **B–D** – Subtabular transverse sections (nos. 14, 12, 7). **E–G** – Calicular transverse sections (nos. 6, 3, 2) [drawings see Fig. 4].

reaching the axis) and become more thickened mainly in their central half (thus changing their former long-triangular to a rectangular appearance – compare Fig. 4N with 4J). They start to melt at their axial ends forming a perfect aulos of cyclothea type (diameter nearly 20% of the corallum), which is interrupted only at the cardinal fossula. The deepest calicular regions occur at the cardinal fossula; there the short and axially free-ending cardinal septum grows longer and touches the neighbouring metasepta.

The secondary subtabular ontogeny starts with a *Neaxon*-like phase (Fig. 4A–C, complete cyclothea, cardinal septum

not shortened). The aulos diameter amounts to 30–35% of the coral; later its width does not increase. The radial orientation of the major septa is very distinct. A succeeding phase (Fig. 4D–G) offers a first, still slight shortening of the cardinal septum and an interruption of the aulos at the fossula. The number of major septa increases from 16 to 23; ephemeral pictures (as Fig. 4B, D) show the four insertion points and allow an easy identification of the six protosepta within the well-orientated sequence of transverse sections. Simple distant tabulae run horizontal or slightly concave within the aulos, and outside fall down against the wall (ca. with 45°,

Fig. 4. *Neosyringaxon michelini* sp. n., holotype no. MNHN.F.A71230 (Paris), lower Frasnian (Pâtures Member of Beaulieu Formation, top of level c), side road ENE Ferques (leading to the Banc Noir and Le Grisset quarries), collection J.-C. ROHART ca. 1975. **A–O** – Series of 15 transverse sections (no. 15–1), subtabular (**A–G**, white lumina filled by “stereoplasma”) and calicular (**H–O**, with few highest subtabular lumina appearing in the centre of J and K, basal calicular regions grey in H and I), with six marked protosepta. **P** – Sketch of corallum (with positions of the prepared transverse sections). **Q** – Two major septa of transverse section 1 (O), showing the rather coarse trabicular microstructure (spines) at their interior margin. [Selected photographs see Fig. 3]. (n = number of major septa, N = number of all septa, d = diameter [in mm]).



Septal formulae:	2 2	3 3	3 3	4 4	4 4
	4 4	4 4	5 4	5 5	6 5
n	16	18	19	22	23
N	24-26	28-30	32	36-37	38
d	2.8-3.0	3.1-3.6	4.2	4.3-6.9	7.0-7.4
Fig.	4A, B	4C, D	4E	4F-L	4M-O

estimated without a longitudinal section). The septal microstructure is clearly trabecular; the axial ends of major septa (Fig. 4Q) prove a spiny upper septal margin (rather coarse, as usual for descendants from the genus *Neaxon*).

Comparisons: The new species differs from *Neosyringaxon elegantum* JIA in JIA et al., 1977 (and its two possible synonyms) in the smaller size; its major septa are thinner than the interseptal spaces in the upper calice. *Neosyringaxon polonicum* (SOBOLEV, 1904) has slightly rhopaloid axial ends of major septa in the lower calice, when melting to construct the cyclotheca (according to the revision of FEDOROWSKI 1965). *Neosyringaxon independense* (STAINBROOK, 1946) is a more slender coral with the cardinal septum situated on the convex side. *Neosyringaxon calvini* (STAINBROOK, 1946) has well-developed short minor septa still in the lower calice. Modern intensive revisions of all those species are necessary in order to find more detailed relationships or differences.

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References

- BARROIS, C. (1882): Recherches sur les terrains anciens des Asturies et de la Galice. – Mémoires de la Société Géologique du Nord, **2** (1): 1–630.
- BERKOWSKI, B. (2008): Emsian deep-water Rugosa assemblages of Hamar Laghdad (Devonian, Anti-Atlas, Morocco). – Palaeontographica, (A), **284** (1–3): 17–68.
- BIRENHEIDE, R. & SOTO, F.M. (1977): Rugose corals with wall-free apex from the Lower Devonian of the Cantabrian Mountains, Spain. – Senckenbergiana Lethaea, **58** (1–3): 1–23.
- BLAINVILLE, H.M.D. DE (1830): Zoophytes. – In: CUVIER, F.G. (ed.): Dictionnaire des Sciences Naturelles. 2. partie, Règne organisé, Zoologie, Zoophytes: 17–32; Strasbourg & Paris (Levrault).
- BRICE, D. (1988): Le Dévonien de Ferques, Bas-Boulonnais (N. France). – Biostratigraphie du Paléozoïque (Université de Bretagne Occidentale, Brest), **7**: 1–522.
- BRICE, D., BULTYNCK, P., COLBEAUX, J.P., LETHIERS, F., MISTIAEN, B., ROHART, J.-C. & BIGEY, F. (1976): Une nouvelle coupe dans le Dévonien de Ferques (Boulonnais, France). – Annales de la Société Géologique du Nord, **96** (2): 135–155.
- BRICE, D., COLBEAUX, J.P., MISTIAEN, B. & ROHART, J.-C. (1979): Les Formations dévoniennes de Ferques (Bas-Boulonnais, France). – Annales de la Société Géologique du Nord, **98** (4): 307–324.
- BRICE, D., MISTIAEN, B. & ROHART, J.-C. (2002): Progrès dans la connaissance des flores et faunes dévoniennes du Boulonnais (1971–2001). – Annales de la Société Géologique du Nord, (2), **9**: 61–74.
- BUSCH, D.A. (1941): An ontogenetic study of some rugose corals from the Hamilton of western New York. – Journal of Paleontology, **15** (4): 392–411.
- CARRUTHERS, R.G. (1913): *Lophophyllum* and *Cyathaxonia*: Revision notes on two genera of Carboniferous corals. – The Geological Magazine, new series, (5), **10** (2): 49–56.
- 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 Königlich Akademie der Wissenschaften zu Berlin, physikalische Abhandlungen, **1832** (1): 225–380.
- FAUROT, L. (1909): Affinités des Tétracoralliaires et des Hexacoralliaires. – Annales de Paléontologie, **4**: 69–108.
- FEDOROWSKI, J. (1965): Lindstroemiidae and Amplexocariniidae (Tetracoralla) from the Middle Devonian of Skały, Holy Cross Mountains, Poland. – Acta Palaeontologica Polonica, **10** (3): 335–355.
- FEDOROWSKI, J. (1986): Permian rugose corals from Timor. – Palaeontographica, (A), **191** (4–6): 173–227.
- FEDOROWSKI, J. (1990): Redescription of the original collection of *Zaphrentis calyculus* Miller, 1891, Rugosa. – Acta Palaeontologica Polonica, **34** (4): 275–325 (dated 1989).
- FEDOROWSKI, J. (2003): Podgromady [subclasses] Rugosa Milne Edwards et Haime, 1850, Dividocorallia Fedorowski, 1991. – In: SARNECKA, E. (ed.): Budowa geologiczna Polski. Tom III. Atlas skamieniałości przewodnich i charakterystycznych. Część 1b-z.1, z.2. Dewon. [Geological structure of Poland. Vol. III. Atlas of index and characteristic fossils. Part 1b, sheet 1-2. Devonian]. – 1–897; Warszawa (Państwowy Instytut Geologiczny) (in Polish).
- FEDOROWSKI, J. (2009): Morphogenesis and taxonomic value of the circumaxial skeleton in Rugosa (Anthozoa). – Lethaia, **42** (2): 232–247. doi: [10.1111/j.1502-3931.2008.00147.x](https://doi.org/10.1111/j.1502-3931.2008.00147.x)
- FEDOROWSKI, J. & SANDO, W.J. (1989): Morphogenesis and relationships of *Trochophyllum* Milne-Edwards and Haime, 1850 (Coelenterata, Anthozoa). – Acta Palaeontologica Polonica, **34** (1): 3–46.
- FOERSTE, A.F. (1888): Notes on Paleozoic Fossils. – Bulletins of the Scientific Laboratories of Denison University (Granville), **3** (2): 117–137.

- FOMICHEV, V.D. (1953): Korally Rugosa i stratigrafiya sredne- i verkhnekamennougol'nykh i permskikh otlozheniy Donetskogo basseyna. [Rugosa corals from the Middle and Upper Carboniferous and from the Permian of the Donez basin]. – Trudy Vsesoyuznyy Nauchno-Issledovatel'skiy Geologicheskii Institut (VSEGEI): 622 pp.; atlas, Moskva (Gosgeolizdat) (in Russian).
- GLINSKI, A. (1963): Neue Gattungen der Metriophyllidae (Rugosa) aus dem Devon des Rheinlands. – Senckenbergiana Lethaea, **44** (4): 321–339.
- GORSKIY, I.I. (1932): Korally iz nizhnnekamennougol'nykh otlozheniy Kirgizskoy stepi. [Corals from the Lower Carboniferous beds of the Kirghiz Steppe]. – Trudy Glavnogo Geologo-razvedochnogo Upravleniya (GGRU), **51**: 1–94 (in Russian).
- GRABAU, A.W. (1928): Palaeozoic Corals of China. Part I. Tetrseptata II. Second contribution to our knowledge of the Streptelasmoid Corals of China and Adjacent Territories. – Palaeontologica Sinica, (B), **2** (2): 1–175.
- HALL, J. (1877): Illustrations of Devonian Fossils: Gastropoda, Pteropoda, Cephalopoda, Crustacea and corals of the Upper Helderberg, Hamilton and Chemung Groups. – Geological Survey of the State of New York (Albany), Palaeontology, 1–7 (dated 1876).
- HILL, D. (1938–1941): A monograph on the Carboniferous rugose corals of Scotland. – Palaeontographical Society Monographs, **91** (412): 1–78 [1938]; **92** (416): 79–114 [1939]; **94** (419): 115–204 [1940]; **95** (424): 205–213 [1941].
- HILL, D. (1939): Western Australian Devonian Corals in the Wade Collection. – Journal of the Royal Society of Western Australia, **25** (8): 141–151.
- HILL, D. (1954): Coral faunas from the Silurian of New South Wales and the Devonian of Western Australia. – Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, **23**: 1–51.
- HILL, D. (1981): Rugosa and Tabulata. – In: TEICHERT, C. (ed.): Treatise on Invertebrate Paleontology, Part F, Coelenterata, Supplement 1: 1–762; Boulder & Lawrence (Geological Society of America & University of Kansas Press).
- HOLWILL, F.J.W. (1964): The coral genus *Metriophyllum* Edwards and Haime. – Palaeontology, **7** (1): 108–123.
- ICZN (1905): International Commission for Zoological Nomenclature: Règles internationales de la nomenclature zoologique adoptées par les congrès internationaux de zoologie (1st edit.). – 57 pp.; Paris (de Rudeval).
- ICZN (1999): International Commission on Zoological Nomenclature, International Code of Zoological Nomenclature (4th edition). – I–XXIX, 1–306; London (Natural History Museum).
- IVANOVSKIY, A.B. (1959): K voprosu o sistematicheskoy polozenii ordovikskikh i siluriyskikh zafrentoidnykh korallov [On the taxonomic position of Ordovician and Silurian zaphrentoidid corals]. – Doklady Akademii Nauk SSSR (Moskva), **125** (4): 895–897 (in Russian).
- JIA, H.-Z., XU, S.-Y., KUANG, G.-D., ZHANG, B.-F., ZUO, Z.-B. & WU, J.-S. (1977): [Anthozoa]. – In: Institute of Geological Sciences of Hubei, Geological Bureaus of Henan, Hubei, Hunan, Guangdong, Guangxi provinces (eds.): Palaeontological Atlas of Central-South China. Part 2. Late Palaeozoic Volume. – I–XII, 1–856; Beijing (Geological Publishing House) (in Chinese).
- JIN, S.-Y. & HE, J.-H. (1982): The Devonian rugose corals of Guangxi, their sequence and systematic descriptions. – In: BAI, S.-L., JIN, S.-Y. & NING, Z.-S. (eds.): The Devonian biostratigraphy of Guangxi and adjacent area. – 109–148, 160–165, 188–202; Beijing (University Press) (in Chinese).
- 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.
- KULLMANN, J. (1965): Rugose Korallen der Cephalopodenfazies und ihre Verbreitung im Devon des südöstlichen Kantabrischen Gebirges (Nordspanien). – Akademie der Wissenschaften und der Literatur, Abhandlungen der mathematisch-naturwissenschaftliche Klasse, **1965** (2): 33–168.
- KUNTH, A. (1869a): Beiträge zur Kenntniss fossiler Korallen. 1. Korallen des schlesischen Kohlenkalkes. – Zeitschrift der Deutschen Geologischen Gesellschaft, **21** (1): 183–220.
- KUNTH, A. (1869b): Beiträge zur Kenntniss fossiler Korallen. 2. Das Wachstumsgesetz der Zoantharia rugosa und über *Calceola sandalina*. – Zeitschrift der Deutschen Geologischen Gesellschaft, **21** (3): 647–688.
- LANG, W.D. & SMITH, S. (1927): A critical revision of the rugose corals described by W. Lonsdale in Murchison's "Silurian System". – The Quarterly Journal of the Geological Society of London, **83** (1–5): 448–491. doi: [10.1144/GSL.JGS.1927.083.01-05.18](https://doi.org/10.1144/GSL.JGS.1927.083.01-05.18)
- LANG, W.D., SMITH, S. & THOMAS, H.D. (1940): Index of Palaeozoic coral genera. – I–VII, 1–231; London (British Museum, Natural History).
- LI, V. DIN'. (1979): *Accurganax* gen. nov. (Rugosa) iz nizhnego devona severo-vostochnoy Fergany. [*Accurganax* gen. nov. (Rugosa) from the Lower Devonian of the North-East Fergana]. – Vestnik Leningradskogo Universiteta, **1979** (18): 107–109 (in Russian).
- LIAO, W.-H. & CAI, T.-C. (1987): Sequence of Devonian rugose coral assemblages from northern Xinjiang. – Acta Palaeontologica Sinica, **26** (6): 689–707 (in Chinese, English summary).
- LIN, B.-Y., XU, S.-Y., JIA, H.-Z., GUO, S.-Z., OUYANG, X., WANG, Z.-J., DING, Y.-J., CAO, X.-D., YAN, Y.-Y. & CHEN, H.-C. (1995): Monograph of Palaeozoic corals. Rugosa and Heterocorallia. – 1–778; Beijing (Geological Publishing House) (in Chinese, English summary).
- LINDSTRÖM, G. (1882): Anteckningar om silurlagren på Carlsöarne. – Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, **39** (3): 5–30.
- LUDWIG, R. (1862): Zur Palaeontologie des Urals. Actinozoen und Bryozoen aus dem Carbon-Kalkstein im Gouvernement Perm. – Palaeontographica, **10** (3, 4): 179–226, 324.
- LUDWIG, R. (1865–1866): Corallen aus paläolithischen Formationen. – Palaeontographica, **14**: 133–244, 249–252.
- MICHELIN, H. (1841–1848): Iconographie Zoophytologique, description par localités et terrains des polyptiers fossiles

- de France et pays environnants. – I–XII, 1–348; Paris (Bertrand).
- MILLER, S.A. (1889–1897): North American Geology and Palaeontology for the use of Amateurs, Students, and Scientists (3rd edit.). – 1–793; Cincinnati & London (Western Methodist Book Concern & Dulau & Co.).
- MILNE-EDWARDS, H. & HAIME, J. (1850–1855): A Monograph of the British Fossil Corals. – Palaeontographical Society Monographs: **I–LXXXV**, 1–322.
- MILNE-EDWARDS, H. & HAIME, J. (1851): Monographie des Polypiers fossiles des terrains paléozoïques, précédée d'un tableau général de la classification des polypes. – Archives du Muséum d'Histoire Naturelle, **5**: 1–502.
- MISTIAEN, B., BECKER, R.T., BRICE, D., DÉGARDIN, J.-M., DERYCKE, C., LOONES, C. & ROHART, J.-C. (2002): Données nouvelles sur la partie supérieure de la formation de Beaulieu (Frasnien de Ferques, Boulonnais, France). – Annales de la Société Géologique du Nord, (2), **9**: 74–84.
- MÜNSTER, G. GRAF ZU (1839): Der *Chiton priscus* und einige andere seltene Versteinerungen aus der Uebergangs-Formation. – Beiträge zur Petrefacten-Kunde, **1**: 38–44.
- NICHOLSON, H.A. & THOMSON, J. (1876): Descriptions of some new or imperfectly understood Forms of Palaeozoic Corals (Abstract). – Proceedings of the Royal Society of Edinburgh, **9** (95): 149–150.
- OLIVER, W.A. JR. (1992): Corals from the Turkey Creek Limestone (Lower Devonian), Southern Oklahoma. – Bulletin of the Oklahoma Geological Survey, **145**: 137–159.
- PEDDER, A.E.H. (1967): Lower Devonian streptelasmatic, lindstroemiid and possible amplexocariniid corals from Victoria. – Proceedings of the Royal Society of Victoria, **80** (1): 107–130.
- POČTA, P. (1902): Anthozoa et Alcyonaires. – In: BARRANDE, J. (ed.): Système Silurien du Centre de la Bohême. Partie I. Recherches Paléontologiques. VIII. 2. – I–VIII, 1–347; Prague (Musée Bohême).
- RIGAUX, E. (1892): Notice géologique sur le Bas-Boulonnais. – Mémoires de la Société Académique de l'arrondissement de Boulogne, **5** (14): 1–108.
- RIGAUX, E. (1908): Le Dévonien de Ferques et ses brachiopodes. – 1–33; Boulogne-sur-Mer (Hamain).
- ROHART, J.-C. (1988): Rugueux Givétiens et Frasnien de Ferques (Boulonnais - France). – In: Brice, D. (ed.): Le Dévonien de Ferques, Bas-Boulonnais (N. France). – Biostratigraphie du Paléozoïque, **7**: 231–296.
- ROHART, J.-C. (2002): Coraux rugueux du Membre des Pâtures, Formation de Beaulieu (Frasnien de Ferques, Boulonnais). – Annales de la Société Géologique du Nord, (2), **9**: 111–127.
- ROHART, J.-C. & WEYER, D. (2020, in press): Revision of *Metriophyllum* Milne-Edwards & Haime, 1851 and *Lindstroemia* Nicholson & Thomson, 1876 (Anthozoa, Rugosa, Devonian).
- RÓZKOWSKA, M. (1969): Famennian Tetracoralloid and Heterocoralloid fauna from the Holy Cross Mountains (Poland). – Acta Palaeontologica Polonica, **14** (1): 1–187.
- RYDER, T.A. (1926): *Pycnactis*, *Mesactis*, *Phaulactis*, gen. nov., and *Dinophyllum*, Lind. – The Annals and Magazine of Natural History, (9), **18** (107): 385–401.
- SARDESON, F.W. (1897): On *Streptelasma profundum* (Owen), *S. corniculum* Hall. – The American Geologist, **20** (5): 277–292.
- SCHINDEWOLF, O.H. (1931): On the genotype and septal development of the coral genus *Petraia* Münster. – The Quarterly Journal of the Geological Society of London, **87** (1–4): 630–649. doi: [10.1144/GSL.JGS.1931.087.01-04.21](https://doi.org/10.1144/GSL.JGS.1931.087.01-04.21)
- SCHINDEWOLF, O.H. (1938): Zur Kenntnis der Gattung *Zaphrentis* (Anthoz., Tetracorall.) und der sogenannten Zaphrentiden des Karbons. – Jahrbuch der Preußischen Geologischen Landesanstalt zu Berlin, **58**: 439–454.
- SCHLOTHEIM, E.F. (1820): Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinertes und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. – I–LXII, 1–437; Gotha (Becker).
- SCHLÜTER, C. (1889): Anthozoen des rheinischen Mittel-Devon. – Abhandlungen zur Geologischen Spezialkarte von Preussen und den Thüringischen Staaten, **8** (4): I–X, 1–207.
- SCHOUPPE, A. v. & STACUL, P. (1959): Säulenlose Pterocoralia aus dem Perm von Indonesisch-Timor (mit Ausnahme der Polycoeliidae). Eine morphogenetische und taxonomische Untersuchung. – Palaeontographica, Supplement-Bände, **4** (5, 4): 197–359.
- SCRUTTON, C.T. (1985): Anthozoa. Rugosa, Heterocoralia, Tabulata. – In: MURRAY, J.W. (ed.): Atlas of Invertebrate Macrofossils: 12–39; London (Longman & The Palaeontological Association).
- 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. (1945): Upper Devonian Corals of the Mackenzie River Region, Canada. – Geological Society of America, Special Papers, **59**: I–VIII, 1–126.
- SOBOLEV, D.N. (1904): Devonskie otlozheniya profilya Gregorzhevitsse-Skaly-Vlokhi. – Izvestiya Varshavskago Politehnicheskago Instituta, **1904** (2): 1–107.
- SOKOLOV, B.S. (1960): Permskie korally yugo-vostochnoy chasti Omolonskogo massiva (s obshchim obzorom plerofiloidnykh rugoz). [Permian corals from the southeastern part of the Omolon massive, with a general review of plerophylloid Rugosa]. – Trudy Vsesoyuznyy Neftyanyy Nauchno-Issledovatel'skiy Geologorazvedochnyy Institut, **154**: 38–77 (in Russian).
- SOSHKINA, E.D. (1928): Nizhnepermskie (artinskies) korally zapadnogo sklona Severnogo Urala. [Die unterpermischen Korallen vom westlichen Abhang des nördlichen Uralgebirges]. – Byulleten' Moskovskogo Obshchestva Ispytateley Prirody, novaya seriya, 36, otdel geologicheskii, **6** (3–4): 339–393; Moskva.
- SOSHKINA, E.D. (1939): Verkhnedevonskie korally Rugosa Urala. [Upper Devonian corals Rugosa of the Ural]. – Trudy Paleontologicheskago Instituta, Akademiya Nauk SSSR, **9** (2): 1–88 (in Russian).
- SOSHKINA, E.D. (1952): Opredelitel' devonskikh chetyrekh-luchevykh korallof. [Determination book of Devonian tetracorals]. – Trudy Paleontologicheskago Instituta (Moskva), Akademiya Nauk SSSR, **39**: 1–127 (in Russian).

- SPASSKIY, N.Y. (1965): Osnovy sistematiki devonskikh chetyrekhluchevykh korallor. [Fundamentals of the systematics of Devonian tetracorals]. – In: SOKOLOV, B.S. & IVANOVSKIY, A.B. (eds.): Rugozy paleozoya SSSR (Trudy 1. Vsesoyuznogo simpoziuma po izucheniyu iskopayemykh korallor SSSR, vypusk 3). – Institut Geologii i Geofiziki, Akademiya Nauk SSSR, Sibirskoe Otdelenie: 80–90; Moskva (Izdatel'stvo Nauka) (in Russian).
- SPASSKIY, N.Y. (1977): Devonskie rugozy SSSR (sistematika, stratigraficheskoe i geograficheskoe znachenie) [Devonian Rugosa of the USSR (systematics, stratigraphical and geographical importance)]. – Ministerstvo Vysshogo i Srednego Spetsial'nogo Obrazovaniya RSFSR: 1–285; Leningrad (Izdatel'stvo Universiteta) (in Russian).
- STAINBROOK, M.A. (1946): Corals of the Independence Shale of Iowa. – *Journal of Paleontology*, **20** (5): 401–427.
- STUCKENBERG, A.A. (1895): Korally i mshanki kamennougol'nykh otlozheniy Urala i Timana. [Korallen und Bryozoen der Steinkohlenablagerungen des Ural und des Timan]. – Trudy Geologicheskago Komiteta, St. Petersburg, **10** (3): 1–244.
- STUMM, E.C. (1949): Revision of the families and genera of the Devonian tetracorals. – *Geological Society of America, Memoirs*, **40**: I–VIII, 1–92. doi: [10.1130/MEM40-p1](https://doi.org/10.1130/MEM40-p1)
- STUMM, E.C. & WATKINS, J.L. (1961): The Metriophyllid coral genera *Stereolasma*, *Amplexiphylum*, and *Stewartophyllum* from the Devonian Hamilton Group of New York. – *Journal of Paleontology*, **35** (3): 445–447.
- SUTHERLAND, P.K. (1965): Henryhouse Rugose Corals. – *Bulletin of the Oklahoma Geological Survey*, **109**: 1–92.
- SUTHERLAND, P.K. (1970): A redescription of the Silurian rugose coral *Syringaxon siluriensis* (McCoy). – *Journal of Paleontology*, **44** (6): 1125–1128.
- TSIEN H.-H. (1970): Espèces du genre *Disphyllum* (Rugosa) dans le Dévonien moyen et le Frasnien de la Belgique. – *Annales de la Société Géologique de Belgique*, **93** (2): 159–182.
- VERRILL, A.E. (1865): Classification of polyps (Extract condensed from a Synopsis of the Polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). – *Proceedings of the Essex Institute, Communications read before the Essex Institute, 1864–1865*, **4**: 145–152.
- WANG, H.-Z. (1950): A revision of the Zoantharia Rugosa in the light of their minute skeletal structures. – *Philosophical Transactions of the Royal Society of London, (B)*, **234** (611): 175–246.
- WANG, H.-Z. & CHEN, J.-Q. (1989a): Microskeletal structures and classification of rugose corals. – *Memoirs of the Association of Australasian Palaeontologists*, **8**: 179–190.
- WANG, H.-Z. & CHEN, J.-Q. (1989b): Chapter 2. Skeletal structures and systematic classification of the subclass Rugosa. – In: WANG, H.-Z., HE, X.-Y., CHEN, J.-Q. et al. (eds.): Classification, evolution, and biogeography of the Palaeozoic corals of China: I–XVII, 6–60, Beijing (Science Press) (in Chinese, English summary).
- WEYER, D. (1970): The Middle Tournaisian Rugose Coral *Zaphrentis delepini* Vaughan 1915. – *Bulletin de la Société Belge de Géologie, Paléontologie et de Hydrologie*, **79** (1): 55–83.
- WEYER, D. (1973): *Famennelasma* gen. nov. (Anthozoa Rugosa) aus der Cephalopoden-Fazies des mitteleuropäischen Oberdevons. – *Paläontologische Abhandlungen, (A)*, **4** (4): 683–688.
- WEYER, D. (1978a): Zwei neue Rugosa-Genera aus dem marokkanischen und thüringischen Devon. – *Jahrbuch für Geologie*, **1973–1974**, (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. (1980): Das silurisch-devonische Rugosa-Genus *Petraia* Münster 1839. – *Freiberger Forschungshefte, C* **357**: 25–41.
- WEYER, D. (1981): Bathyale Rugosa (Anthozoa) aus pelagischem Oberem (Unterdevon) im Thüringischen Schiefergebirge. – *Abhandlungen und Berichte für Naturkunde und Vorgeschichte*, **12** (3): 23–73.
- WEYER, D. (1985): Zur Kenntnis eurasiatisch-nordafrikanischer Emsium/Eiflium-Hapsiphyllidae (Anthozoa, Rugosa; Devon). – *Abhandlungen und Berichte für Naturkunde und Vorgeschichte*, **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*, **15**: 9–24.
- WEYER, D. (1996): *Nichlavalla sytovae* n. g. n. sp. aus dem Lochkovian von Podolien (Anthozoa, Rugosa; Unterdevon, Ukraine). – *Abhandlungen und Berichte für Naturkunde*, **19**: 83–103.
- WEYER, D. (2000): Revision der Gattung *Czarnockia* Rózkowska, 1969 (Anthozoa, Rugosa; Oberdevon). – *Abhandlungen und Berichte für Naturkunde*, **21**: 75–107.
- WEYER, D. (2001): *Muenstraia*, ein neues Rugosa-Genus (Anthozoa) aus dem Obersilur und Unterdevon. – *Mitteilungen aus dem Museum für Naturkunde in Berlin, Geowissenschaftliche Reihe*, **4**: 71–82. doi: [10.5194/fr-4-71-2001](https://doi.org/10.5194/fr-4-71-2001)
- WEYER, D. (2008): Revision des Ludwig/Kunth-Gesetzes zur Septeninsertion der Supraordo Rugosa (Anthozoa, Ordoviz–Perm). – *Abhandlungen und Berichte für Naturkunde*, **30**: 85–145.
- WEYER, D. (2016): Review of some Frasnian ahermatypic coral localities from Germany and description of a new genus *Spinaxon* (Anthozoa, Rugosa, Upper Devonian). – *Geologica Belgica*, **19** (1–2): 147–163. doi: [10.20341/gb.2015.020](https://doi.org/10.20341/gb.2015.020)
- YE, G. & WANG, Z.-P. (1983): New genus and species of Early Carboniferous tetracorals from Jiangyou, Sichuan province. – *Earth Science, Journal of Wuhan College of Geology*, **1983** (4): 85–93, 172–173 (in Chinese, English summary).
- YOH, S.-S. (1937): Die Korallenfauna des Mitteldevons aus der Provinz Kwangsi, Südchina. – *Palaeontographica, (A)*, **87** (1–2): 45–76.
- YU, C.-M. (1957): On the occurrence of a new rugose coral from the Middle Ordovician of Sinkiang province, N.W. China. – *Acta Palaeontologica Sinica*, **5** (2): 307–324 (in Chinese, English summary).

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Addresses of the authors:

DIETER WEYER, Museum für Naturkunde (Leibniz-Institut) an der Humboldt-Universität, Invalidenstrasse 43, 10115 Berlin, Germany;

e-mail: dieter.weyer@t-online.de

Jean-Claude ROHART, 90, rue Claude Gardelain, 59149 Dunkerque, France;

e-mail: jclauderohart@outlook.com