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Article

Revision of *Metriophyllum* Milne-Edwards & Haime, 1850 and *Lindstroemia* Nicholson & Thomson, 1876 (Anthozoa, Rugosa, Devonian)

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With 12 figures

Abstract: *Metriophyllum* has already been "revised" several times (based on "topotypes" from Ferques, Boulonnais, northern France), but nobody was aware of the existence of two different homoeomorphic genera in the local Frasnian, and the wrong morphology (not identical with the lost lectotype) was chosen. New collections allow to propose a neotype for the type species *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850 (middle Frasnian Ferques Formation). Main diagnostic features are: trabicular septal microstructure, 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). The older "*Metriophyllum*-II" (lower Frasnian Beaulieu Formation) has no triad and will be revised as a new, not congeneric species in a separate publication. *Lindstroemia* had been proposed without locality data; hence, nobody could provide topotypes. Some originally included pseudocolumellate Ordovician and Silurian species are meanwhile transferred to *Dalmanophyllum* Lang & Smith, 1939 and *Bodophyllum* Neuman, 1969 (suborder Streptelasmatina). Nicholson's type series (Royal Museum of Scotland, Edinburgh) is labelled "Erie, New York". Later, these common noncolumellate Rugosa (upper Hamilton Group, Givetian) were described as *Stereolasma rectum* (Hall, 1843) and *Lopholasma carinatum* Simpson, 1900. Two syntype sections are chosen as lectotype specimen of the type species *Lindstroemia columnaris* Nicholson & Thomson, 1876, thus declaring the genus as senior synonym of *Lopholasma* Simpson, 1900 – both now junior synonyms of *Metriophyllum*. Most published so-called *Metriophyllum*/*Lindstroemia*/*Lopholasma* species (Silurian–Permian) are very poorly known and must be restudied morphologically; for the moment they have – homeless like a *nomen nudum* – no reasonable definite generic place. The new taxonomy accepts a family Lindstroemiidae Počta, 1902 (synonyms: Metriophyllidae Hill, 1939, Stereolasmatidae Fomichev, 1953). Also suborder names, as used in today's best handbooks, must be changed. The former Metriophyllina Spasskiy, 1965 lose their name-giving taxon and are renamed Cyathaxoniina Spasskiy, 1977. *Metriophyllum* becomes a member of the Zaphrentoidina Wang, 1950 (synonyms: Metriophyllina Spasskiy, 1965, Stereolasmatina Hill, 1981, Hapsiphyllina Nudds in Nudds & Löser, 2001).

Key words: Ahermatypic Givetian–Frasnian corals, taxonomy, Cyathaxoniina, Zaphrentoidina (*Metriophyllum*, *Lindstroemia*, *Lopholasma*, *Stereolasma*), morphology (metriophylloid carinae).

1. Introduction

Many ancient Rugosa genera are still waiting for redefinitions after revisions of their type and topotype materials – in spite of the enormous amount of work already done in this field through the world. Among countless pioneers, we all remember the outstanding efforts of the British school around William Dickson Lang (1878–1966) and Stanley Smith (1883–1955), summarized in the catalogue of Lang et al. (1940). Urgent future tasks are cases such as *Densiphyllum* Dybowski, 1873 (Silurian), *Tryplasma* Lonsdale, 1845 (Devonian) or *Tachylasma* Grabau, 1922 (Permian), concerning derived family names (Densiphyllinae

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Dybowski, 1873, Tryplasmatidae Etheridge, 1907, Tachylasmatidae Grabau, 1928) and even a suborder name (Tachylasmatina Fedorowski, 1973).

Our revision is based on new, well-stratified collections (Rohart 1974–1977, Rohart & Weyer 1993) in the lower–middle Frasnian of Ferques near Boulogne-sur-Mer, the type locality of the type species *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850. The related and often discussed taxa *Lindstroemia* Nicholson & Thomson, 1876 and *Lopholasma* Simpson, 1900 from the Givetian Hamilton Group of New York are no longer classified as separate genera; they become doubtless synonyms of *Metriophyllum* Milne-Edwards & Haime, 1850.

Abbreviations: CS – transverse section, LS – longitudinal section, TS – thin section, P – Peel, R – remaining part, d – diameter, n – number of major septa (protosepta and metasepta), N – number of all septa (major septa, minor septa = catasepta, but excluding hyposepta).

The studied corals are deposed in the Muséum Nationale d'Histoire Naturelle (Histoire de la Terre) Paris, France (MNHN-F-), in the Royal Museum of Scotland Edinburgh, UK (RMS-), and in the Museum für Naturkunde (Leibniz-Institut) at Humboldt University Berlin, Germany (MB.K.).

2. Genus *Metriophyllum* Milne-Edwards & Haime, 1850

Milne-Edwards & Haime shortly diagnosed their new taxon (1850: LXIX) and almost simultaneously (1851: 317, pl. 7, figs. 1–2) provided a more detailed definition together with a well-illustrated description of the designated type species *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850 from the Devonian of Ferques near Boulogne-sur-Mer (France). This was done in a period before the introduction of thin-section technics for Palaeozoic corals, which started nearly 20 years later in Germany (with Kunth 1869a and Fischer-Benzon 1871). Lang et al. (1940: 84) stated (without argumentation, but correctly) that the original proposal of *Metriophyllum bouchardi* included two taxa; they restricted the species by choosing a lectotype (Fig. 1.1, 1a, non Fig. 2, 2a). Both specimens are definitely lost – as communicated in 2019 by Dr. J.-M. Pacaud, Muséum National d'Histoire Naturelle (Histoire de la Terre) in Paris, where the Henri Milne-Edwards collection is stored.

Milne-Edwards & Haime (1851: 318) wrote that material of *Metriophyllum bouchardi* was deposed in "Mus. de Paris, Bouchard-Chantereaux, Mi-

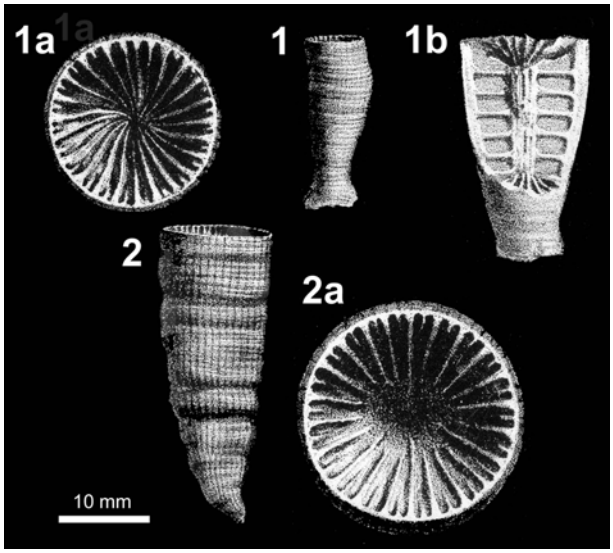


Fig. 1. Syntypes of *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850 (copied from Milne-Edwards & Haime 1851, pl. 7, figs. 1, 2), "Dévonien, Ferques près Boulogne" (Boulonnais, northern France). 1 and 2 in natural size; 1a, 1b and 2a "enlarged". **1, 1a.** Lost lectotype (designated Lang et al. 1940: 84), probably middle Frasnian Ferques Formation. **2, 2a.** Lost paralectotype (not congeneric with the lectotype, as already stated by Lang et al. 1940: 84), representing a separate genus, provisionally named "*Metriophyllum*-II" in Weyer (1991: 11, 1996: 86), to be revised in a forthcoming separate publication), probably lower Frasnian Beaulieu Formation. The specimen is quite homoemorphic with the lectotype and the herein proposed neotype, but seems to belong to another suborder (Cyathaxoniina Spasskiy, 1977, family Petraiidae Koninck, 1872. These illustrations had been prepared in a period before the introduction of thin section technics for coral studies, at that times using only well-preserved specimens with free calices, broken fragments, and polished surfaces. Figures "given by Milne-Edwards & Haime are remarkably faithful" (Carruthers 1913: 50, an opinion achieved after his investigations of their collections in Paris, 1907). The calice picture of the lectotype (1a) shows an absolutely reliable configuration of the septal apparatus and its symmetry (shortened cardinal septum below, two long counter minor septa forming a triad with the counter septum above), precisely observed by the ancient authors years before the proposals of Ludwig (1865), Kunth (1869b), Sardeson (1897) and Faurot (1909), now called the law of Kunth (or better Ludwig-Kunth-law – Weyer 2008) ruling the ontogenetic septal insertion of Rugosa. Both features (antiseptal triad, shortened cardinal septum) are missing in the calice figure of the paralectotype (2a), thus indicating another generic taxon, which occurs in a slightly older horizon according to our new, better stratified collections.

chelin". Their now lost specimens "Mus. de Paris" surely had been a donation of Nicolas Robert Bouchard-Chantereaux (1802–1864), géologue and malacologiste, well known for his generous zoological-palaeontological presents to other specialists – Frasnian brachiopods of his collection from Ferques still are preserved in Paris (MNHN-F). Further parts of his collections were stored in the muséum of Boulogne-sur-Mer, where he lived, being its director), but that institution suffered seriously during the war (1939–1945), and no small Devonian coral of the *Cyathaxonia* facies could be found.

Jean-Louis Hardouin Michelin (1786–1867) had described the first corals from the Middle–Upper Devonian of Ferques, but in his collections (also in Paris, MNHN-F) only one specimen survived (Rohart 1988: 231): "*Cyathophyllum profundum* Michelin, 1845", revised in Rohart & Semenoff-Tian-Chansky (1981: 2) as *Pseudoacervularia profunda* (Michelin, 1845). The species was re-assigned to *Potyphyllum* Coen-Aubert, 2016 (p. 169), but must be renamed, being a homonym of the Permian (Wuchiapingian) *Cyathophyllum profundum* Geinitz, 1842 = *Calophyllum columnare* (Schlotheim, 1813). Lower–middle Frasnian dysphotic/aphotic coldwater corals from Ferques were also published 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); this now lost material was renamed by Milne-Edwards & Haime (1850: LXIX, 1851: 318) as *Metriophyllum bouchardi*.

Later, the genus *Metriophyllum* became the base for a family Metriophyllidae Hill, 1939, and for a suborder Metriophyllina Spasskiy, 1965. There had been five attempts to revise the taxon, based on topotypes. The first (Barrois 1882: 196) 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) and others. Smith (1945), Holwill (1964), Weyer (1970) and Scrutton (1985) illustrated "topotypic" specimens with occasional aulos and without an antiseptal triad. Hill (1981: F190) relied on this opinion.

Such current views on the taxonomy of *Metriophyllum* suffer from these inadequate revisions based on mistaken "topotypes", which are not congeneric with the lectotype illustration. New, well stratified collections, organized by the Université Catholique in Lille (under Denise Brice) for a comprehensive revision of the Givetian–Frasnian stratigraphy and palaeontology at Ferques (resulting in the monograph of Brice 1988; Mistiaen et al. 2001), demonstrated the presence of not only one ahermatypic Rugosa genus *Metriophyllum* in the Frasnian. In addition, Rohart (1988, 2002, in Brice et al. 2002, in Mistiaen et al. 2002) recorded species of *Catactotoechus* Hill, 1954, and *Metrioplexus* Glinski, 1963, and he indicated their different stratigraphic positions within the Frasnian of the Boulonnais (Fig. 2). In addition, Weyer & Rohart (2020) found *Neosyringaxon* Jia, 1977. Today, intensive serial sectioning is indispensable in order to determine such externally indistinguishable small corals. We also had to learn that historical fossil samples, distributed in several 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 before in the unsuccessful case of *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850.

Using the new collections of J.-C. Rohart (received in 1981), the presence of two different, quite homoeomorphic Metriophyllids in different stratigraphic levels near Ferques was already mentioned by Weyer (1991: 11, 1996: 86).

"*Metriophyllum*-I" (middle Frasnian upper Ferques Formation) – with cardinal fossula and long counter septal 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; here our Fig. 1, 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, as the youngest "minor septum" at every of the four insertion points always is a morphogenetical major septum).

"*Metriophyllum*-II" (lower Frasnian Beaulieu Formation) – with aulos, without antiseptal triad and fossula. Nearly all "topotypic" cross sections of *Metriophyllum bouchardi* published up to now (Smith 1945; Holwill 1964; Weyer 1970; Scrutton 1985; Rohart 2002) belong to this group, but are a misinterpretation in view of the lost *bouchardi*-lectotype (and its neotype, proposed here). At that time, these authors were not aware of the existence of two homoeomorphic, but dif-

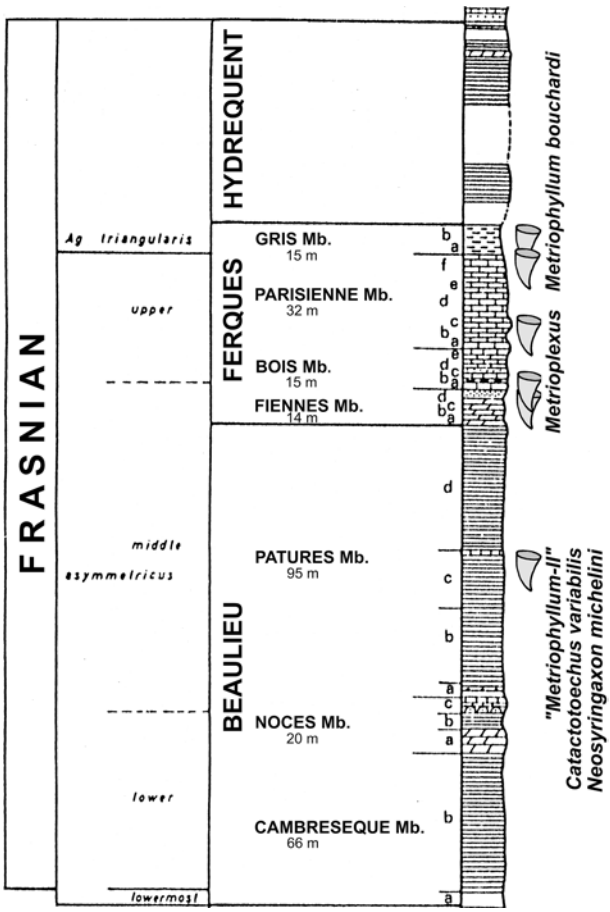


Fig. 2. Frasnian sequence of Ferques (Boulonnais, northern France) – lithostratigraphy with conodont data (after Brice 1988:11, fig. 2) and ahermatypic Rugosa (according to stratified new collections).

ferent genera with metriophylloid carinae in the local Frasnian of Ferques. All specimens studied by Smith (1945) came from the older Beaulieu Formation. There are no reliable stratigraphic data in Holwill (1964). He even had indicated a Middle Devonian age and declared that he collected extensively at Ferques, but nearly all figured specimens of his "*Metriophyllum bouchardi*" are from the older collections of E. Rigaux (1872–1880, 1882, 1908) and S.G. Percival (1913) in the British Museum of Natural History, London (according to the acquisition catalogue, kindly submitted by J.G. Darrell). Always it had been easier to find the rare small Rugosa in the older Beaulieu Formation than to collect the extremely rare corals in the younger Ferques Formation – they are represented in our collections in relationship 4:1. 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 Schouppé & Stacul 1959). The family taxon Metriophyllidae Hill, 1939 is a senior synonym of Stereolasmatidae Fomichev, 1953, but a junior synonym of Lindstroemiidae Počta, 1902. 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).

3. Genus *Lindstroemia* Nicholson & Thomson, 1876

The genus has been proposed in an abstract publication – nowadays such a procedure would be a priori invalid as a *nomen nudum* (according to the actual code of zoological nomenclature, ICZN 1999), but at that time it was valid in the sense of the first International Code of Zoological Nomenclature (ICZN 1905, Zoological Congress in Monaco), following common zoological rules of the 19th Century. A nearly meaningless and (in view of the now available type material) rather incorrect "diagnosis" and no precise locality/age data (only "Devonian rocks of North America") did not allow a recognition for a long period of nearly a century.

Nicholson & Etheridge (1878: 80, fig. 4) seemed to have satisfactorily improved the insufficient introduction of *Lindstroemia* in 1876, but the type species *Lindstroemia columnaris* Nicholson & Thomson, 1876 "is still unpublished" (Nicholson & Etheridge 1878: 81), though first illustrations (fig. 4b, b') with some few explanatory words were offered. This "better" concept of the genus was based mainly on an Upper Ordovician–Silurian group of Rugosa bearing a well-developed pseudocolumella, which (only according to present knowledge: senior synonym of *Lopholasma* Simpson, 1900) is absent in the type species (in spite of the chosen name *Lindstroemia columnaris*).

These older taxa are *Lindstroemia laevis* Nicholson & Etheridge, 1878, *Petraia subduplicata* McCoy, 1850, and *Cyathaxonia dalmani* Milne-Edwards &

Haime, 1851; the last one had already been separated as genus *Centrotus* Lindström in Thomson & Nicholson, 1876 more or less at the same time as the proposal of *Lindstroemia*, but that name was preoccupied by *Centrotus* Fabricius, 1803 (Insecta, Hemiptera) and became replaced by *Dalmanophyllum* Lang & Smith, 1939. Nicholson & Etheridge (1878) classified *Lindstroemia* as Cyathaxoniidae Milne-Edwards & Haime, 1850, which then included also *Cyathaxonia siluriensis* McCoy, 1850, type species of *Syringaxon* Lindström, 1882 (subfamily Laccophyllinae Grabau, 1928), today seen as the direct ancestor of *Cyathaxonia* Michelin, 1847 (Weyer 1996: 85). 1878 those so-called representatives of *Lindstroemia* seemed to be closest to *Cyathaxonia*; at present there are no longer ideas about relationships, because the Dalmanophyllinae Lecompte, 1952 are Streptelasmatina Wedekind, 1927, characterized by central septal lobes (axial synapticulae – Weyer 1972: 711).

Neuman (1969: 55–56) tried to find an interpretation of the type species *Lindstroemia columnaris*, only based on the illustrations of Nicholson & Etheridge (1878, fig. 4b, b'; here refigured as Fig. 3.1a, 3a), suggesting for the transverse section perhaps *Metriophyllum* Milne-Edwards & Haime, 1850 (as Lang et al. 1940: 77) or eventually *Syringaxon* Lindström, 1882, for the longitudinal section a similarity with *Stereolasma* Simpson, 1900 (as Stumm 1949: 7). He stated: "the presence or absence of a calicular boss cannot be ascertained from the figured sections". *Lindstroemia subduplicata* (McCoy, 1850) from Scotland (Girvan district, Craighead Limestone = upper Ordovician, Caradoc, and Mulloch Hill Sandstone = basal Llandovery, lower Rhudannian) was tentatively assigned to his new genus *Bodophyllum* Neuman, 1969 (Dalmanophyllinae).

Grabau (1928: 111) preferred a change of the type species for *Lindstroemia* and favoured the upper Ordovician–Silurian taxa with a pseudocolumella (now *Bodophyllum* Neuman, 1969 and *Dalmanophyllum* Lang & Smith, 1939), as the Devonian type species from North America apparently was never described. Coral literature presents several pre-Devonian so-called "*Lindstroemia*" species (even from USA and Australia: Foerste 1906, Chapman 1932), mostly not well analyzed morphologically and never revised to a modern level of taxonomy. Also the Devonian *Lindstroemia minima* Spasskiy, 1960 from Russia and even Permian species as *Lindstroemia permiana* Girty, 1908 (USA) cannot be classified according to actual systematics. *Lindstroemia lingulifera* Foerste, 1906 (Silurian) was not sectioned, but the calice (with pseudocolumella) is like a *Dalmanophyllum*.

A family Lindstroemiidae was proposed by Počta (1902) to include in addition 1. *Nicholsonia* Počta, 1902 (pre-occupied coral name: Schlüter 1885) = *Alleynia* Počta, 1902 = junior synonym of *Syringaxon* Lindström, 1882, and 2. *Barrandeophyllum* Počta, 1902 (both now separated as Laccophyllidae Grabau, 1928 – Hill 1981: F191). His *Lindstroemia transiens* Počta, 1902 (upper Emsian) is doubtful and must be restudied. Independently, Scheffen (1933) introduced also (as new) Lindstroemiidae for Silurian Dalmanophyllinae. The family name Lindstroemiidae was not used by Stumm (1949: 6), Soshkina & Kabakovich (1962: 321) and Spasskiy (1977: 83) in favour of Metriophyllidae Hill, 1939, clearly due to the imperfect knowledge about the genus *Lindstroemia*, but it reappeared in Glinski (1963), followed by Fedorowski (1965: 336), Pedder (1967: 110), Birenheide (1978: 23), Różkowska (1969: 32, as superfamily Lindstroemiicae). Hill (1981: F201) was more cautious: "until the type material is restudied, *Lindstroemia* will be unsuitable as the name genus for a family".

This wanted type material of Nicholson & Thomson (1876) is now available (Figs. 3, 4) and demonstrates that Nicholson had received a small sample of the typical Givetian ahermatypic Rugosa fauna, richly occurring in the shaly facies of the upper Hamilton Group in the state of New York (USA), as described by Stumm & Watkins (1961). The presence of the material (as part of the Nicholson collection) in the Royal Museum of Scotland in Edinburgh was announced by its catalogue of Benton (1979), but surely known already somewhat earlier, as W.A. Oliver jr. (then Washington) perhaps for the first time restudied these corals in 1968.

In 1986, we received photographs of all syntype thin sections of *Lindstroemia columnaris* Nicholson & Thomson, 1976 by the kind help of Colin Scrutton (then Newcastle-upon-Tyne) – they include the three species *Lopholasma carinatum* Simpson, 1900, *Stereolasama rectum* (Hall, 1843), and *Amplexiphyllum hamiltoniae* (Hall, 1877), abundant in Erie county; and we are able to choose a lectotype. In 1968, W.A. Oliver jr. had already donated several specimens of *Lopholasma* and *Stereolasma*, which here are used for comparison purposes; they helped already for the phenomenon of hyposepta (Weyer 1980, 1997).

There exist eight thin sections (6CS, 2LS) in the Nicholson collection. Seven can be reconstructed to

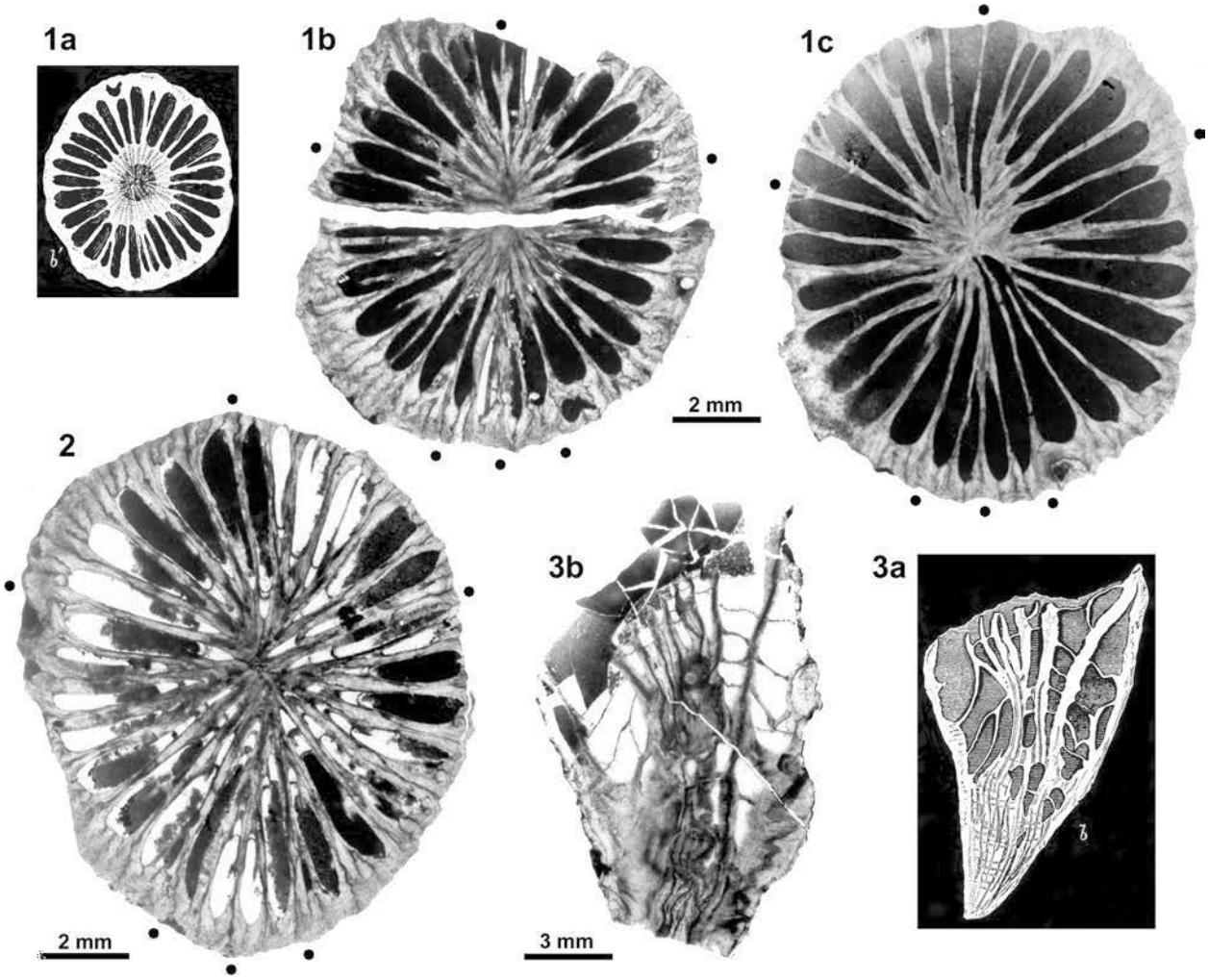


Fig. 3. Some syntypes of *Lindstroemia columnaris* Nicholson & Thomson, 1876, "Devonian rocks of North America" (Nicholson & Thomson 1876: 150), emended to Hamilton Group (Givetian), Erie County (western New York State, USA) according to the original label in the Nicholson collection, its catalogue (Benton 1979), and oral information 1981 (to D. Weyer) by W.A. Oliver jr. about abundant localities (Brett et al. 1983, fig. 1) yielding the unique *Stereolasma* assemblage (Busch 1941, Stumm & Watkins 1961) in the shaly Marcellus facies of Erie County (Oliver & Sorauf 1983: 48). **1a–c.** *Metriophyllum columnare* (Nicholson & Thomson, 1876), lectotype, RMS-Edinburgh nr. 1968.15.41a,42d. 1a. Copy of the slightly schematic drawing of Nicholson & Etheridge (1878, fig. 4b'), the first illustration of the species. 1b. The same thin section in correct protoseptal orientation, x6. 1c. A further thin section (hitherto unpublished, erroneously numbered 1968.15.2d, but clearly belonging to the lectotype, x6. **2.** Transverse section of a paralectotype specimen (erroneously numbered 1968.15.42b, but clearly another individual as Fig. 1c), x6. **3a–b.** *Stereolasma rectum* (Hall, 1843), longitudinal section without metriophylloid carinae, RMS-Edinburgh nr. 1968.15.43b, original drawing (3a) of Nicholson & Etheridge (1878, fig. 4b) and new photograph of this thin section, x6. This syntype and two further ones (here not studied and illustrated) of *Amplexiphyllum hamiltoniae* (Hall, 1877) (nr. RMS-Edinburgh 1968.15.41b,42a) demonstrate that Nicholson had a small collection of the three very common Hamiltonian ahermatypic Rugosa (*Stereolasma* Simpson, 1900, *Lopholasma* Simpson, 1900 = *Lindstroemia*, *Amplexiphyllum* Stumm, 1949), which he united under *Lindstroemia columnaris*. Bill Oliver studied all syntypes of *Lindstroemia columnaris* in 1968 and temporarily wanted to propose the longitudinal section of Fig. 3b as lectotype, which he thought to be undeterminable; then the genus *Lindstroemia* Nicholson & Thomson, 1876 (and the family names Lindstroemiidae Počta, 1902, and Lindstroemiidae Scheffen, 1933) perhaps would become nomina dubia for ever, and *Lopholasma* Simpson, 1900 with better known type material might remain available. He did not publish this opinion, but started the still missing modern revision of the *Stereolasma* coral association from the Givetian Hamilton Group; he was well aware of the insufficient taxonomy even after the proposal of new taxa by Busch (1941) and their perhaps unjustified synonymy (without reasonable arguments) in Stumm & Watkins (1961). In future, after such a revision the isolated longitudinal section of Fig. 3b really could become undeterminable; its attribution to *Stereolasma rectum* reflects only the actual restricted state of knowledge.

come from four specimens. There are no doubts about the identification of two of the thin sections with the illustrations from 1878, which are slightly schematic(!) drawings:

1. *Lindstroemia columnaris* Nicholson & Thomson, 1876, here designated as lectotype.
CS 1968.15.41a. Fig. 3.1b, figured by Nicholson & Etheridge 1878, fig. 4b'
CS 1968.15.42d. Fig. 3.1c
2. *Lindstroemia columnaris* Nicholson & Thomson, 1876, here designated as paralectotype
CS 1968.15.42b. Fig. 3.2
CS 1968.15.42c. Not figured (coral broken into five fragments)
3. *Stereolasma rectum* (Hall, 1843)
LS 1968.15.43b. Fig. 3.3b, figured by Nicholson & Etheridge 1878, fig. 4b
4. *Amplexiphyllum hamiltoniae* (Hall, 1877)
CS 1968.15.41b. Not figured
CS 1968.15.42a. Not figured
5. indeterminable fragment (? of 3. *Stereolasma rectum* (Hall, 1843)
LS 1968.15.43a. Not figured

Thus, *Lopholasma* Simpson, 1900 becomes a junior synonym of *Lindstroemia* Nicholson & Thomson, 1876 by this lectotype fixation, as already declared or suspected several times; both genera are based on the same species. This implies a possible identity of *Lindstroemia* with *Metriophyllum* Milne-Edwards & Haime, 1850, as sometimes postulated for *Lopholasma* (Hill 1939; Smith 1945; Holwill 1964; Pedder 1967; Różkowska 1969). At first we tried to separate *Lindstroemia* from *Metriophyllum* by its strongly shortened cardinal septum, situated in a more distinctly developed fossula, but the cardinal septum is also shortened (less strong) in the here revised type species *Metriophyllum bouchardi*. On the other hand there exist undescribed *Metriophyllum*-like plesiomorph species with always unshortened long cardinal septum – their presence was predicted by the Tournaisian successor *Drewerelasma* Weyer, 1973 (Weyer 1994, figs. 7–8, study of the primary calyx-ontogeny), which differs from its Devonian ancestors in the loss of trabiculae (septal margins smooth, not spinous – non-trabicular trend of Weyer 2014: 121). Perhaps a new genus will be proposed for such corals from the Frasnian of Thuringia (Weyer 2016, fig. 1). Both *Lindstroemia* and *Lopholasma* are now synonyms of *Metriophyllum*, within the family Lindstroemiidae Počta, 1902 (with synonyms Metriophyllidae Hill, 1939, Stereolasmatidae Fomichev, 1953).

The Hamiltonian *Stereolasma* fauna was not restricted to the Devonian palaeogeographical faunal realm of the eastern United States. It occurred also in the European faunal province through marine exchanges in Morocco and Mauretania (unpublished samples of typical *Amplexiphyllum* and *Stereolasma*, Dra valley and Tafilalt, D. Weyer collection). The new Moroccan record supports the coral migration route from the Eastern North American Appohimchi subprovince towards Northwestern Africa, as suggested by Oliver (1975: 156, fig. 4, 1976, fig. 5, 1977); originally based on hermatypic taxa of the photic zone, but obviously also valid for ahermatypic faunas of deeper/colder waters.

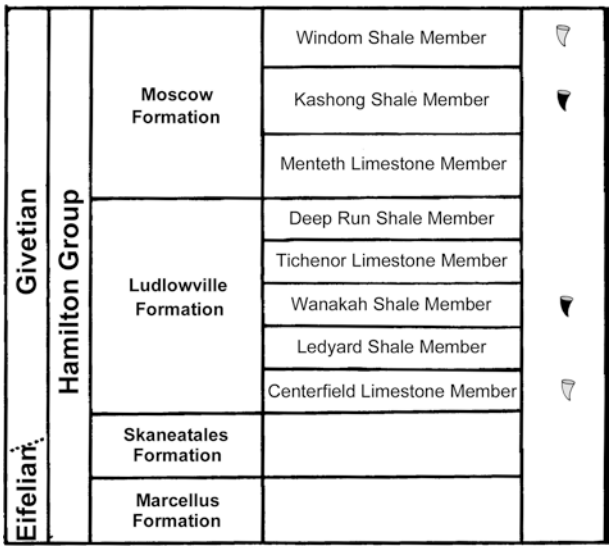
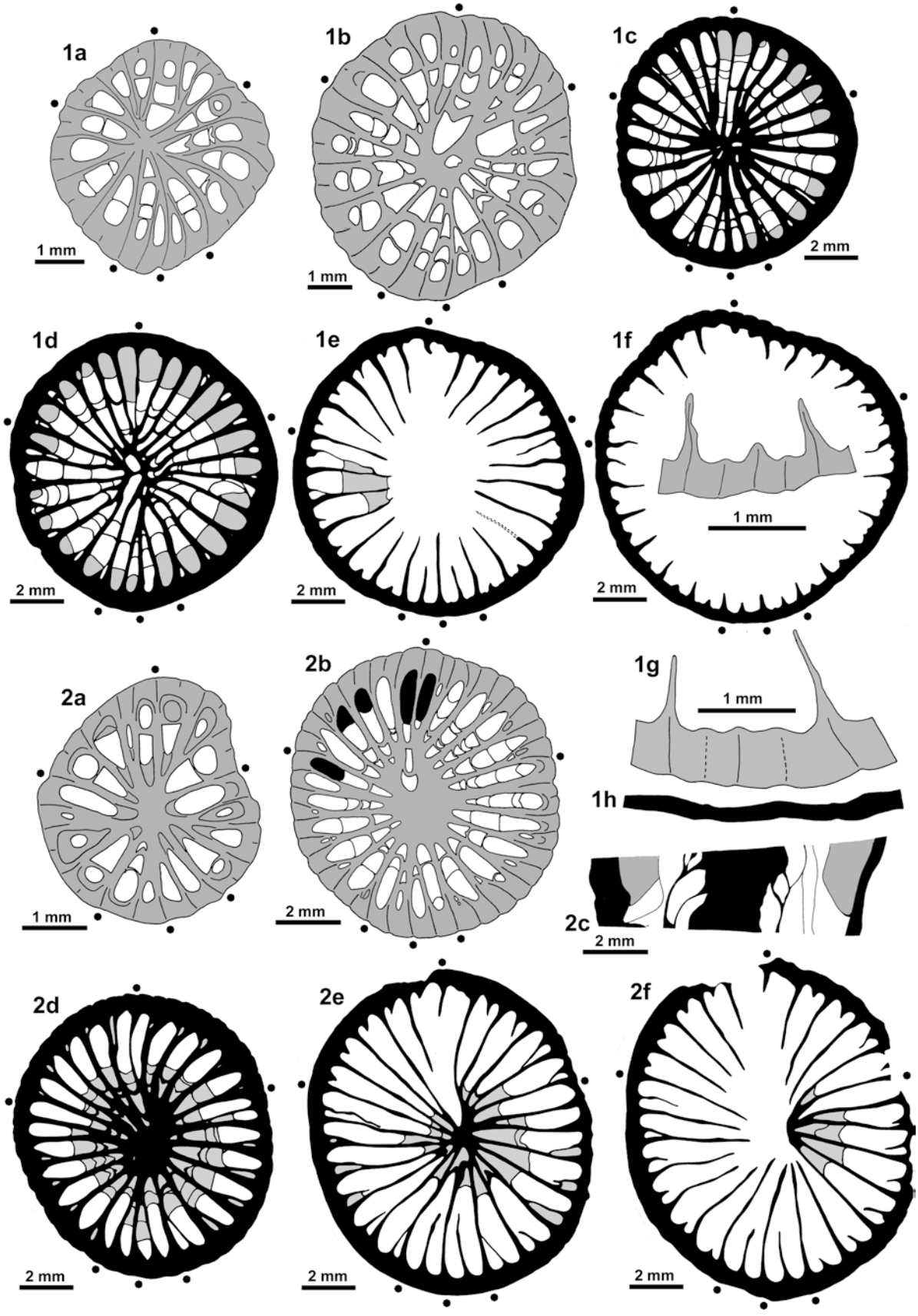


Fig. 4. Distribution of Rugosa of the *Stereolasma* community in the Givetian Hamilton Group of western New York State (after Brett et al. 1983; black coral symbols indicate small samples available for our studies).

Fig. 3 (continued)

septal formulae:

6 I 5	5 I 5
8 I 8	7 I 8
n 31	n 29
N 55	N 51
d 10.2×9.4, 11.2×10.1 mm	d 12.4×10.6 mm
Fig. 1b, 1c	Fig. 2


1a
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1g
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2f
2 mm

Several species of "*Lopholasma*" had been described from Upper Carboniferous and Permian strata in Europe and Asia. The real generic position of all these Rugosa is unknown. Their descriptions and illustrations allow no interpretations – no serial sections, no chance to identify the protosepta, often fragmentary or badly preserved material, all only with metriophylloid carinae.

Upper Carboniferous: *Lopholasma carbonaria* Grabau, 1922, *Lopholasma taiyuanense* Yu & Wang, 1987, *Lopholasma cratoseptatum* Zhao & Liang, 1989, *Lopholasma simplex* Wu & Lin, 1992.

Permian: *Lopholasma gracile* Soshkina, 1928, *Lopholasma ilitschense* Soshkina, 1928 (Felser 1937; Heritsch 1933; Kostic-Podgorska, 1965).

A difficult problem is the supposed identity of *Lopholasma* Simpson, 1900 and *Stereolasma* Simpson, 1900 (Easton 1944: 31, being even conspecific according to Smith 1945: 28, 1952: 305). Stainbrook (1946: 410) and Stumm (1949: 7) opposed this view, and we concur with them. But W.A. Oliver jr. "warned" D. Weyer (orally) not to exaggerate the taxonomical value of metriophylloid carinae, when he started an intensive study of the Hamilton Group Rugosa (including the *Stereolasma* faunas). Serial sections of both type species demonstrate not only the difference in absence or presence of carinae, but also a second diagnostic feature. *Stereolasma rectum* (Hall, 1843) has longer contratingent minor septa in mature stages, as usual joined with a biform tabularium (Figs. 5, 12.1–2); this was already shown by Brown (1907, figs. 10–13). The minor septa – excepting the counter septum triad – in mature sections of *Metriophyllum carinatum* (Simpson, 1900) disappear in the basal calice by stereoplasmatic thickening of the archaeothecal wall and are never contratingent (Fig. 6). This reduction or stunting is well visible in excellent preserved specimens without stronger recristallisations (Fig. 6.2a). Growth lines within the wall indicate a stop of minor septal length inside the wall; if there occur "projections" into the interseptal lumina, then these are always metriophylloid carinae imitating minor septa (without any connection of the dark median line; Fig. 6.2a, three lumina of the left counter quadrant near the lateral septum). Such structures should be controlled for the thin section drawing of Simpson (1900, fig. 19).

Of course, for the moment it is unknown, if there exist morphological changes throughout Hamiltonian times within the life span of these two species

Fig. 5. *Stereolasma rectum* (Hall, 1843), Wanakah Shale Member (Ludlowville Formation, lower Givetian) of Hamilton Group, Athol Springs (5 miles S of Buffalo, near Lake Erie, New York State), donation of W.A. Oliver jr. 1968. **1.** Specimen MB.K.8071. 1a–f. Serial transverse sections nrs. 11, 9, 7, 5, 4, 3 (a–b subtabular, c–d with peripheral basal calicular grey lumina, e with few uppermost subtabular grey areas), x9 (a), x8 (b), and x5 (c–f), 1f (insert). 1g–h. Details of upper calicular transverse sections nrs. 3 and 1 (2 metasepta, 1 cataseptum, 2 hyposepta, all visible within the calice and by their septal furrows also on the external archaeotheca), x18. Photographs see Fig. 12.1a–c.

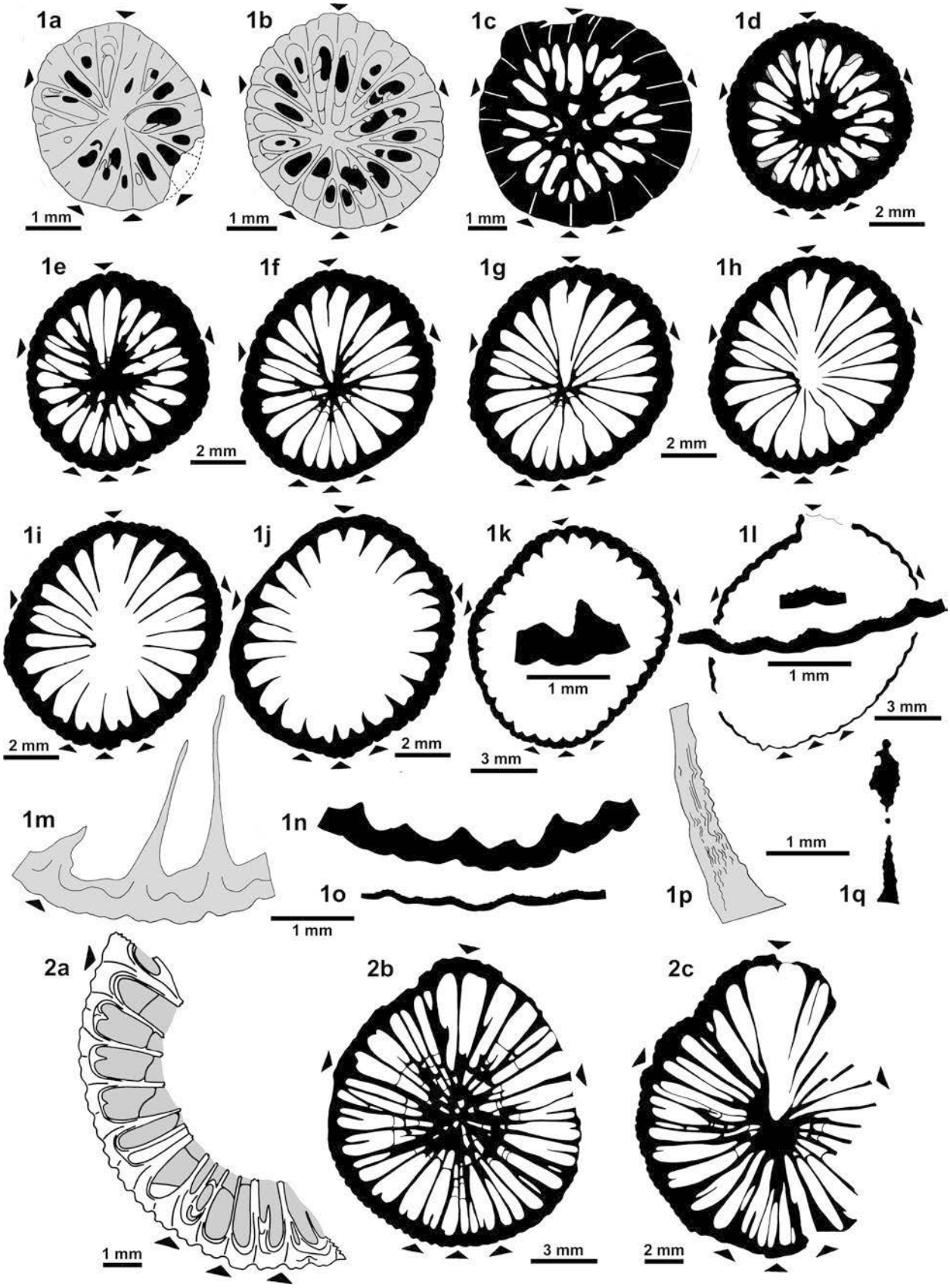
septal formulae:

3 I 3	3 I 3	5 I 5
5 I 4	5 I 5	7 I 7
n 19	n 20	n 28
N 30	N 34	N 48
d 4.6×4.8 mm	d 6.1×6.6 mm	d 8.8×8.8–11.4 mm
Fig. 1a	Fig. 1b	Fig. 1c–f

2. Specimen MB.K.8072. 2a. Early subtabular transverse section nr. 19, x12; 2b. Transverse section nr. 10 at calicular base (black interseptal lumina of fossula and left cardinal quadrant filled with calicular sediment), x6. 2c. Median longitudinal section nr. 8 (calicular part grey), x6. 2d–f. Adult lower calicular transverse sections nrs. 6, 3, 1 (grey subtabular regions in the centre, and in position I of contratingent minor septa: few in 2e, all in 2d excepting the antiseptal triad), x5. Photographs see Fig. 12.2.

septal formulae:

3 I 3	4 I 5	5 I 5	5 I 5
4 I 4	6 I 6	6 I 7	7 I 8
n 18	n 25	n 27	n 29
N 28	N 44	N 47	N 50
d 3.4×3.7 mm	d 8.2×8.8 mm	d 9.6×10.4 mm	d 10.8×13.2
Fig. 2a	Fig. 2b	Fig. 2d	Fig. 2e–f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1 mm
1q
2a
1 mm
2b
3 mm
2c
2 mm

(Fig. 4). Such intensive studies (planned and started by Oliver) are still necessary (after Busch 1941 and Stumm & Watkins 1961). They could also prove, if the later synonymisations of Busch's new taxa are really justified. Our restricted materials of *Stereolasma* come only from the Wanakah Shale Member.

4. Revised taxonomy

Class Anthozoa Ehrenberg, 1834
Subclass Zoantharia Blainville, 1830
Superorder Rugosa Milne-Edwards & Haime, 1850
Order Stauriida Verrill, 1865

Suborder Zaphrentoidina Wang, 1950

Synonyms: Metriophyllina Spasskiy, 1965; Stereolasmatina Hill, 1981; Hapsiphyllina Nudds in Nudds & Löser, 2001.

Remarks: The present International Code of Zoological Nomenclature (ICZN 1999) does not yet include names of the order level, but their common use respects the basic laws of priority. Wang (1950: 203) did not mention any authorship for suborders and families, but later (Wang & Chen 1989a: 187, 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, because he had classified *Hapsiphyllum* Simpson, 1900 as a subgenus of *Zaphrentoides* Stuckenberg, 1895). Schouppé & Stacul (1959) again proposed a suborder name Zaphrentoidina as new taxon.

Family Lindstroemiidae Počta, 1902

Synonyms: Metriophyllidae Hill, 1939; Stereolasmatidae Fomichev, 1953.

Genera: *Metriophyllum* Milne-Edwards & Haime, 1850 (synonyms *Lindstroemia* Nicholson & Thomson, 1876; *Lopholasma* Simpson, 1900); *Stereolasma* Simpson, 1900; *Nichlavalla* Weyer, 1996; *Saleelasma* Weyer, 1970; *Drewerelasma* Weyer, 1973 (? with junior synonym *Parametriophyllum* Wang Zeng-Ji, 1993) – probably also ? *Metrioplexus* Glinski, 1963, ? *Fuchuanelasma* Kullmann & Liao,

Fig. 6. *Metriophyllum columnare* (Nicholson & Thomson, 1876), donation W.A. Oliver jr. 1968. **1.** Specimen nr. MB.K.8074, Kashong Shale Member, Moscow Formation, Little Beards Creek (near Genesee, western New York State). 1a–l. series of transverse sections (nrs. 22, 20, 18, 16, 15, 13–9, 7, 2), x10 (a), x9 (b), x7 (c), x5 (d–j), x4 (k, l, inserts x15). 1m. detail of 1j, x15, with shortened cardinal septum, three metasepta (the last one hidden in the wall), and two catasepta (also reduced inside the archaeotheca); the former presence of these three minor septa, now visible by growth lines in the wall, is also indicated by the biform wall thickness of one interseptal lumen (wall thicker at the antiseptal side = position I and thinner at the cardinal side = position II sensu Sutherland 1965), 1n, 1o. Septal details of transverse sections 7 and 1 (external furrows of major and minor septa deeper than those of hyposepta, distinct multitrabicular septal margins in 1o, active hyposepta within the lumen at the uppermost calice rim), x15. 1p, 1q. Trabiculae in the upper calice (longitudinal sections 6 and 5, radial-median in one septum and tangential), x15. Photographs of the specimen see Fig. 12.

septal formulae:

3 I 3	3 I 3	3 I 4	4 I 4	4 I 4
4 I 4	5 I 5	5 I 5	6 I 6	7 I 6
n 18	n 20	n 21	n 24	n 25
N 29	N 32	N 36	N 40–41	N 43
d 3.0×3.3 mm	d 4.0×4.2 mm	d 5.4 mm	d 6.6×6.8–8.2x8.6 mm	d 9.3×10.0 mm
Fig. 1a	Fig. 1b	Fig. 1c	Fig. 1d–j	Fig. 1k

2. Specimen nr. MB.K.8075, Moscow Shale (lower part), Kidders (NW of Ithaca, western New York State). 2a. Part of subtabular transverse section (nr. 6), demonstrating well preserved external septal furrows of the archaeotheca (protosepta, metasepta, catasepta, hyposepta), minor septa (excepting the two long counter minors of the antiseptal triad) reduced in a lower calice phase and visible only within the wall, x7. 2b, c. Lower calicular transverse sections (nrs. 4, 2), x4 and x3.5.

septal formulae:

5 I 5	5 I 5
7 I 7	7 I 8
n 28	n 29
N 49	N 50
d 12.8 mm	d 15.1 mm
Fig. 2b	Fig. 2c

1985, – questionable ? *Metrionaxon* Glinski, 1963 (perhaps better classified in Laccophyllinae Grabau, 1928 within Cyathaxoniidae Milne-Edwards & Haime, 1850).

Distribution: For the moment, *Nichlavalla* seems to be the oldest member (Lochkovian). Presumed Silurian and even Late Ordovician records (mostly as *Lindstroemia*) – omitted in the later following list of species ever assigned to *Metriophyllum*, *Lopholasma*, *Lindstroemia* – were based mainly on Dalmanophyllinae, following Nicholson & Etheridge (1878). Without a modern revision, today they all are undeterminable using only the available published data (Foerste 1906; Chapman 1925; Ladd 1929; Scheffen 1933). The youngest known taxa occur in the upper Tournaisian–lower Viséan: *Saleelasma*? *axiferum* (Hudson, 1943).

Remarks: The taxonomical significance of metriophylloid carinae is valued controversely (Fedorowski 1987: 33) – mostly seen as suitable feature to define genera, but sometimes also judged as intrageneric or even intraspecific variation (best example: Smith 1945: 28, 1952: 305 – proposing the synonymy of *Stereolasma* Simpson, 1900 and *Lopholasma* Simpson, 1900). Comparable doubles are *Claviphyllum* Hudson, 1942 and *Clavilasma* Weyer, 1975 (Antiphyllidae Iljina, 1970) or *Calophyllum* Dana, 1846 and (?) *Calocarinophyllum* Zeng in Zeng & Cai, 1983 (Polycoeliidae Fromentel, 1861), distinguished only (?) in the presence or absence of metriophylloid carinae. Rich populations of Permian *Calophyllum* (Russian Lower Kazanian = Roadian/Wordian, European Zechstein = middle Wuchiapingian) never posess such carinae, which rarely occur in the mid-Permian *Calophyllum rarum* (Niermann, 1975) of Timor (restudied by Weyer, unpublished). But the mid-Carboniferous type species *Calocarinophyllum vesiculosum* Zeng in Zeng & Cai, 1983 (NW China) is also defined to acquire adult lonsdaleioid dissepiments (Lin et al. 1995: 724). In these cases, a generic separation of carinae-bearing species really might be unnecessary, though worthy for the often not easy distinction between real minor septa (genetic: catasepta sensu Ezaki 1989) and metriophylloid carinae, which appear after the Lindstroemiidae in several unrelated families of Late Carboniferous–Permian times (Asserculiniidae Fedorowski, 1986: *Asserculinia* Schouppé & Stacul, 1959, *Duplocarinia* Fedorowski, 1986; Lophophyllidiidae Moore & Jeffords, 1945: *Lophocarinophyllum* Grabau, 1922; Tachylasmatidae Grabau, 1928: *Carinotachylasma* Xu in Jia et al., 1977).

Genus *Metriophyllum* Milne-Edwards & Haime, 1850

Synonyms: *Lindstroemia* Nicholson & Thomson, 1876; *Lopholasma* Simpson, 1900.

Type species: *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850, by monotypy.

Emended diagnosis: Small conical, often slightly cornute corals (cardinal septum situated mostly on the convex side). Calice funnel-shaped (non-evert), with radially positioned major septa reaching the centre, there united in an axial stereozone (no everted axial boss or pseudocolumella). Archaeotheca mostly longitudinally ribbed, with furrows of major and minor septa (pinnately arranged as schizosepta), sometimes also with intercalate hyposeptal furrows. Septal microstructure trabicular (multitrabicular on the broad peripheral septal sockets at the calicular rim, later simply monacanth in the middle and lower calice). Length of major septa nearly uniform; only the cardinal septum is shortened in the calice (reaching the axial stereozone just near the base of the cardinal fossula). Tetracoralloid pinnate arrangement of major septa occasionally visible at the four insertion points (only for a short time after increase of new septa). Two neighbouring minor septa of the counter septum adult long and connected to a triad, which starts rather early in the youth. All other minor septa are active as small projections into the lumen only in upper calice phases; later in the lower calice they stop their growth and become secondarily reduced by continuous stereoplasmatic thickening of the archaeotheca, where they still remain visible in cases of missing or weak recristallisations. Calicular and subtabular interseptal lumina always (even in juvenile phases) distinctly broader (twice or more) than the major septa; this space is used by few to many metriophylloid carinae, which start in the middle calice and run at right angle to the upword growth direction. Simple tabulae (sometimes also rare tabellae) are axially domed (moderate–strong); no dissepiments.

Relationships: The refined taxonomy of *Metriophyllum*-like *Rugosa* – started with Glinski (1963) – requires the separation of further new genera, using such features as septal microstructure (trabicular or fibro-normal), length of cardinal septum, development of minor septa (disappearing during calyx-ontogeny or contratingent), antiseptal triad, normal or biform tabularium. Several such deviating morphologies are now studied (mainly of Givetian–Frasnian age). The difficult proof of missing trabiculae in Carboniferous–Permian times was successful in *Saleelasma* Weyer, 1970 and *Drewerelasma* Weyer, 1973, but it is still unknown, whether trabiculae survived the global Hangenberg-Event or even sometimes were already lost during the Devonian in some Lindstroemiidae. The actual poor morphological knowledge of most so-called "*Metriophyllum*" species (see the following list) does not allow a precise classification – therefore, their majority is judged either as doubtful or as surely excluded. This is understandable, as many older taxa were introduced in a past period thinking that one transverse and one longitudinal section are enough to define a species. But today intensive serial sectioning like in the classical pioneer studies of Carruthers (1908, 1910) is indispensable to find the basic diagnostic features (trabiculae, shortened cardinal septum in a fossula, antiseptal triad, disappearance of other minor septa in the lower calice remaining only hidden within the archaeotheca, clear differentiation between septa and carinae), connected with a doubtless identification of the six protosepta, often veiled by the disturbing metriophylloid carinae.

The few true representatives of *Metriophyllum* (in the here revised sense) in that list were investigated by preparation of available collections in our hands. Materials of *Lopholasma tullium* Williams, 1935 (middle Givetian, Tully Limestone, New York State) were kindly presented to D. Weyer by C.E. Brett (Cincinnati). A. Ehling (Berlin) helped with a

loan of the Weyer-1974 collection, at that time "top-secret": *Metriophyllum* sp. 1, Weyer 2016 (151, fig. 4.A1–6), lower Frasnian, borehole Binz 1/1973, southeastern Baltic Sea Island of Rügen.

Species of *Metriophyllum*:
Metriophyllum bouchardi Milne-Edwards & Haime, 1850 (Frasnian)
Lindstroemia columnaris Nicholson & Thomson, 1876 (Givetian)
Lopholasma carinatum Simpson, 1900 (Givetian) (= synonym of *Metriophyllum columnare*)
Lopholasma tullium Williams, 1935 (Givetian)
Metriophyllum sp. Weyer, Feist & Girard, 2003 (Frasnian)
Metriophyllum sp. 1 Weyer, 2016 (Frasnian)

Doubtful species of *Metriophyllum* and its synonyms:
Metriophyllum laeve Schlüter, 1889 (Eifelian)
Metriophyllum poshiense Mansuy, 1912 (Middle Devonian)
Lopholasma delawarense Baker, 1942 (Givetian?)
Metriophyllum deminutivum Easton, 1944 (lower Tournaisian)
Metriophyllum iowense Stainbrook, 1946 (Frasnian)
Metriophyllum smithi LeMaître, 1952 (Eifelian)
Metriophyllum lituum Holwill, 1964 (Frasnian)
Metriophyllum skalense Fedorowski, 1965 (Givetian)
Metriophyllum solidum Pedder, 1967 (Emsian)
Metriophyllum devexicarinatum Pedder, 1967 (Lower Devonian)

Species excluded from *Metriophyllum* and its synonyms:
Metriophyllum battersbyi Milne-Edwards & Haime, 1851 (Givetian)
Metriophyllum gracile Schlüter, 1884 (Eiflian) = *Metrionaxon* Glinski, 1963
Metriophyllum elsii Whidborne 1901 (Middle Devonian)
Metriophyllum? *irregulare* Paeckelmann, 1922 (Frasnian)
Lopholasma carbonaria Grabau, 1922 (Late Carboniferous)
Lopholasma gracile Soshkina, 1928 (Artinskian)
Lopholasma ilitschense Soshkina, 1928 (Artinkian)
Lindstroemia? *cornuhirci* Weissermel, 1939 (Famennian)
Metriophyllum volki Weissermel, 1939 (Frasnian)
Metriophyllum cruciferum Weissermel, 1941 (Emsian)
Metriophyllum? *minor* Spriestersbach, 1942 (Eifelian)
Lindstroemia (Schindewolfia) lauterbergensis Weissermel, 1943 = *Barrandeophyllum* Počta, 1902 (?Emsian)
Metriophyllum sp. A Smith, 1945 (Frasnian)
Metriophyllum erisma Hill, 1950 = type species of *Haptophyllum* Pedder, 1967 (Emsian)
Metriophyllum murrindalense Pedder, 1967 (Emsian)
Metriophyllum soshkinae Różkowska, 1969 (Artinskian)
Metriophyllum album Soto, 1975 (Upper Emsian)
Metriophyllum qaganqulutense Guo, 1980 (Early Permian)
Metriophyllum xinjiangense Zeng in Zeng & Cai, 1983 (Late Carboniferous)
Metriophyllum aequale Zeng in Zeng & Cai, 1983 (Late Carboniferous)
Metriophyllum honacoense Erina, 1984 (Givetian)
Metriophyllum longlinense Zheng, 1986 (Late Carboniferous)
Metriophyllum omhaense Liao & Cai, 1987 (Lower Tournaisian) = ? *Drewerelasma*
Metriophyllum curviseptatum Liao & Cai, 1987 (Lower Tournaisian) = ? *Drewerelasma*
Metriophyllum henanense Ding in Xia & Ding, 1987 (Carboniferous)
Lopholasma taiyuanense Yu & Wang, 1987 (Late Carboniferous)
Lopholasma cratoseptatum Zhao & Liang, 1989 (Late Carboniferous)
Metriophyllum qijiagouense Wang & Yu, 1989 (Late Carboniferous)
Metriophyllum minor Wang & Yu, 1989 (Late Carboniferous)
Lopholasma simplex Wu & Lin, 1992 (Late Carboniferous)
Metriophyllum rozkowskae Fedorowski, 2003 (Famennian)
Metriophyllum? sp. 2 Weyer, 2016 (Frasnian)
Metriophyllum sp. Weyer, 2016 (Frasnian)

Remarks: At the moment, corrected generic assignments are mostly impossible for the majority of these species; if proposed, they are based on revisions or suggestions by D. Weyer (1977 – *Lindstroemia lauterbergensis*; unpublished – *Metriophyllum gracile*). The *Metriophyllum omhaense* Assemblage (also including *Metriophyllum curviseptatum*) of northern Sinkiang (NW China) was dated by Liao & Cai (1987: 703) as latest Famennian, but in reality is already basal Tournaisian, proved by a *Protognathodus* conodont fauna, younger than the global Hangenberg extinction event (Sartenaer & Han 1990). The stratigraphical situation resembles those in Germany (Saalfeld in Thuringia, Drewer in the northern Rhenish Mountains), where *Drewerelasma* appeared at the Carboniferous base, following a general trend of Rugosa (in the sense of Lang 1923): distributed loss of trabiculae and change to fibro-normal septal microstructure (Kato 1963) at this time level. Therefore, a coral from the *Acutimitoceras acutum* ammonoid Zone (*Eosiphonodella sulcata* conodont Zone) in Thuringia was determined as *Drewerelasma* sp. aff. *curviseptatum* (Liao & Cai, 1987) (Weyer 2001: 70, fig. 3.2a–b).

Some species groups will be recognized in future as separate genera. One example are taxa with the plesiomorph feature of a never shortened long cardinal septum (like the oldest Lindstroemiidae: *Nichlavalla* Weyer, 1996) – such now studied corals are known in the Frasnian of Thuringia. Another group might be species with the apomorph feature of longer contratingent/contracline free minor septa as "*Metriophyllum*" *murrindalense* Pedder, 1967, achieving this progressive development already in Emsian times. Seemingly, *Parametriophyllum* Wang Zeng-ji, 1993 (Early Tournaisian) and *Neometriophyllum* Ding, 1985 (Early Permian) are also such acceptable genera excluded from *Metriophyllum*, but the first is probably (due to unstudied septal microstructure) a junior synonym of *Drewerelasma* Weyer, 1973, and the poorly analyzed second (see Lin et al. 1995: 383, 739, fig. 503) is not a member of Lindstroemiidae.

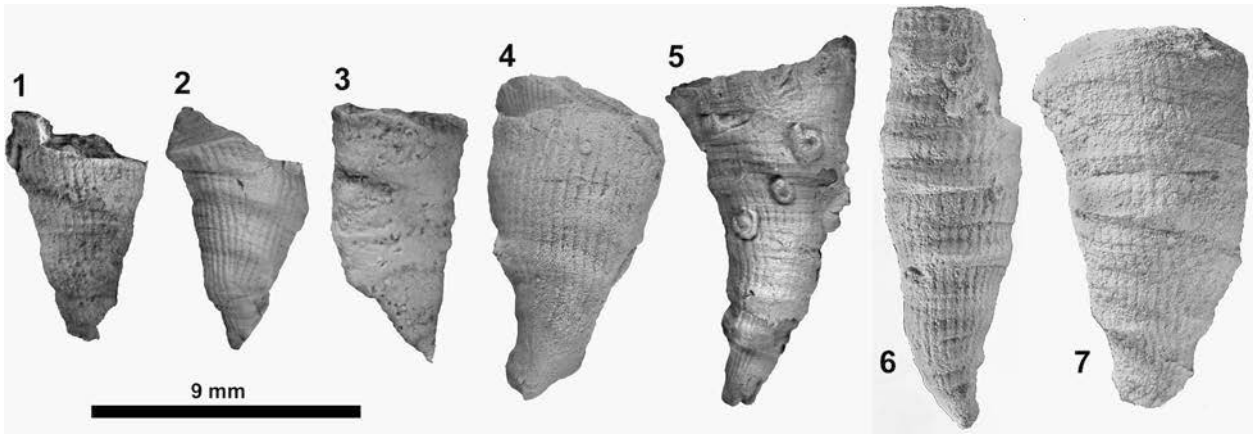


Fig. 7. *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850, polypar photographs of correct topotypes (new collections of J.-C. Rohart 1974–1977 and J.-C. Rohart & D. Weyer 1993), x2, all from La Parisienne quarry east of Ferques (1, 3, 4, 6, 7 western face, 2 eastern entrance, 5 southern slope), middle Frasnian Ferques Formation (1, 3, 4, 6, 7 Gris Member; 2, 5 Parisienne Member). There are nearly no external differences against other generic taxa. 1. nr. MNHN-F-A71901, 2. nr. MNHN-F-A71905, **3**. MNHN-F-A71902, 4. nr. MB.K.8079, 5. nr. MB.K.8081, 6. nr. MNHN-F-A71904, 7. nr. MB.K.8078. For selected photographs and drawings of sections see Figs. 8–10.

Metriophyllum bouchardi Milne-Edwards & Haime, 1850

Figs. 1.1, 1a, 7.1–7.7, 8a–k, 9a–j, 10.1–10.8

? 1845 *Cyathophyllum mitratum*. – Michelin, p. 183, pl. 47, fig. 7. [non Schlotheim 1820].
pars 1850 *Metriophyllum Bouchardi* nob. – Milne-Edwards & Haime, p. LXIX.
pars 1851 *Metriophyllum bouchardi*. – Milne-Edwards & Haime, p. 318, pl. 7, fig. 1, 1a, 1b, non 2, 2a.
?non 1882 *Metriophyllum Bouchardi* Mil. Edw. et H. – Barrois, p. 196, pl. 7, fig. 2a–d.
pars 1940 *Metriophyllum bouchardi* Edwards & Haime, 1850. – Lang et al., p. 84.
?non 1945 *Metriophyllum bouchardi* Edwards and Haime. – Smith, p. 29, pl. 1, figs. 11–13, pl. 34, figs. 1a–e.
pars 1949 *Metriophyllum bouchardi* Edwards and Haime. – Stumm, p. 7, 60, pl. 3, figs. 1–2 [lectotype, copy from 1851], non pl. 3, figs. 3–7 [copied from Smith 1945].
non 1964 *Metriophyllum bouchardi* Edwards and Haime 1850. – Holwill, p. 111, pls. 16, fig. 6, 17, figs. 1–6, 11, 18, figs. 7,11, 19, fig. 4.
non 1969 *Metriophyllum* aff. *bouchardi* M.Edw.-H., 1850. – Różkowska, p. 37, pl. 2, fig. 4, fig. 8.J,K_1–K_2. (renamed *Metriophyllum rozkowskae* Fedorowski, 2003).
non 1969 *Metriophyllum bouchardi* Ed. et H., 1850. – Tsien, p. 140, pls. 1, fig. 6, 2, fig. 9, 37, fig. 5.
non 1970 *Metriophyllum bouchardi* Edwards & Haime 1850. – Weyer, p. 57, pl. 1, figs. 1–6, 2, figs. 1–2.
non 1977 *Metriophyllum bouchardi* Edwards et Haime. – Spasskiy, p. 83, pl. 25, fig. 1a–b.
non 1983 *Metriophyllum bouchardi qitaiense* subsp. n. – Cai in Zeng & Cai, p. 113, pl. 31, fig. 2.
non 1985 *Metriophyllum bouchardi* Edwards & Haime. – Scrutton, p. 22. fig. 3.3.29A, B.
pars 1988 *Metriophyllum bouchardi* M.-E. et H., 1851. – Rohart, p. 233.
non 1992 *Metriophyllum* cf. *bouchardi* Milne-Edwards & Haime 1850. – Birenheide & Soto, p. 103, pl. 3, figs. 16–17.
pars 2002 *Metriophyllum bouchardi* M. E. & H., 1850. – Rohart in Brice et al., p. 66.
pars 2002 *Metriophyllum bouchardi* M.-Edw. & H., 1850. – Rohart in Mistiaen et al., p. 79, fig. 2.
non 2002 *Metriophyllum bouchardi* Milne-Edwards et Haime 1850. – Rohart, p. 112, pl. 5, fig. 1a–b.

Types: Lectotype (designated by Lang et al. 1940: 84) – the specimen figured by Milne-Edwards & Haime 1851, pl. 7, fig. 1, 1a (Devonian, Ferques near Boulogne, France); this coral is lost ("probably" – Holwill 1964: 112; actual information 2019 by J.-M. Pacaud, custody of the Muséum Nationale d'Histoire Naturelle, Paris, where collections of Henri Milne-Edwards (1800–1885) are deposed.

Neotype (here proposed): specimen nr. MNHN-F-A71901 (Figs. 7.1, 8a–k, 10.2a–b, former collection number 634-1), Muséum Nationale d'Histoire Naturelle, Paris, collection J.-C. Rohart 1974, middle Frasnian Ferques Formation (Gris Member, terms a–b), western face of La Parisienne quarry ENE of Ferques near Boulogne-sur-Mer. [9 duplicate peels nr. MB, K, 8076 in Berlin].

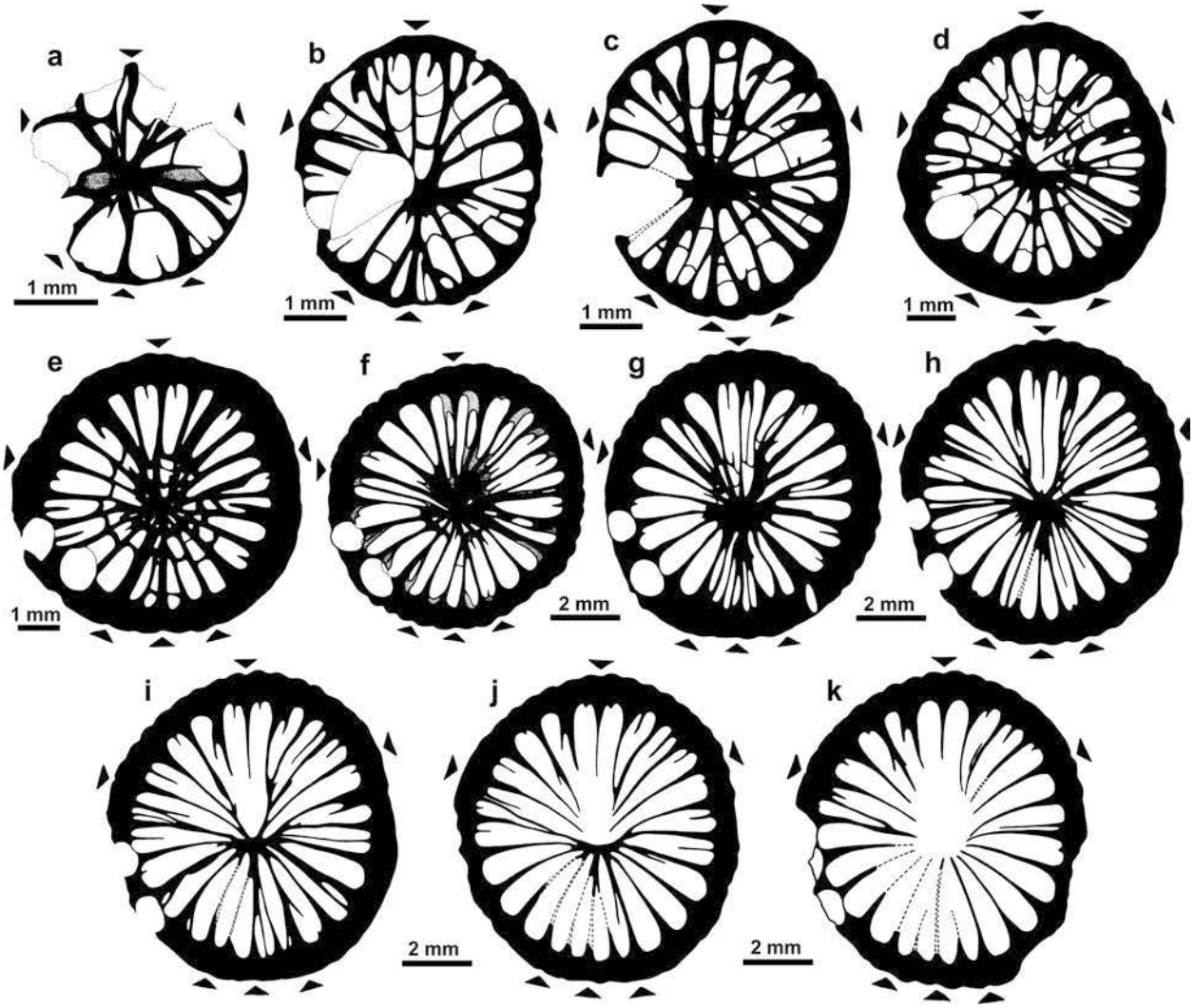


Fig. 8. *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850, neotype, middle Frasnian Ferques Formation (Gris Member, term a–b), La Parisienne quarry east of Ferques (western face), nr. MNHN-F-A71901 (duplicate peels nr. MB.K.8076), collection J.-C. Rohart 1974. **a–k**. Series of transverse sections (a–d subtabular, e–k calice; nrs. 1, 3–5,7–9,11–14), x12 (a), x9 (b, c), x7 (d), x6 (e) and x5 (f–k). For photographs see Figs. 7.1, 10.2a–b.

Septal formulae:

2 I 2	3 I 3	4 I 4	4 I 4	4 I 4
3 I 4	4 I 4	5 I 5	6 I 6	6 I 7
n 15	n 18	n 22	n 24	n 25
N 22	N 30	N 36	N 41	N 42
d 2.7 mm	d 3.8×4.2 mm	d 3.9×4.6 mm	d 6.7–8.2 mm	d 8.7–9.0 mm
Fig. a	Fig. b	Fig. c	Fig. e–g	Fig. h–k

Further material: Eight specimens (in addition to the neotype), from three localities and two different horizons near Ferques (see map in Weyer & Rohart 2020, fig. 2):

a) Revised type locality (according to our neotype designation) – La Parisienne quarry, western face. Gris Member (terms a, b) of the Ferques Formation, collections J.-C. Rohart 1974, J.-C. Rohart & D. Weyer 1993.

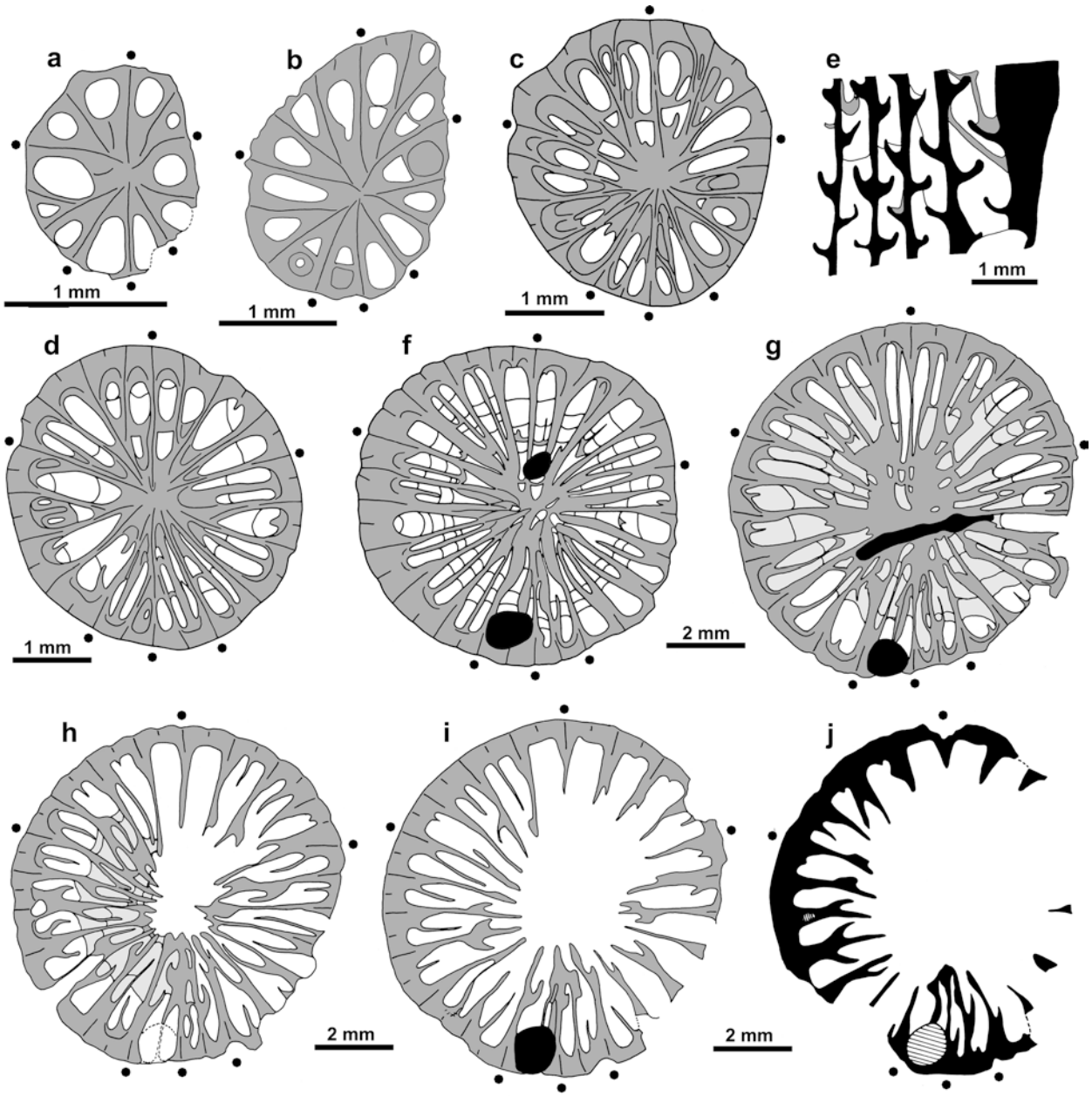


Fig. 9. *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850, Ferques Formation (Gris Member), La Parisienne quarry east of Ferques (western face), topotype specimen nr. MNHN-F-A71902 (duplicate peels: nr. MB.K.8077), collection J.-C. Rohart 1974. **a–j**. Serial transverse sections (nrs. 21, 19, 17, 15, 7, 5, 4, 3, 2) and tangential longitudinal section (nr. 12), x25 (a), x18 (b), x15 (c), x12 (d), x10 (e), x6 (f–j). For photographs see Fig. 10.4a–d.

septal formulae:

2 I 2	3 I 3	3 I 3	4 I 4	4 I 4
4 I 3	4 I 4	5 I 5	7 I 6	7 I 7
n 15	n 18	n 20	n 25	n 26
N 22	N 28–29	N 34	N 42–43	N 44
d 1.1x1.2 mm	d 2.2–2.9 mm	d 3.8 mm	d 8.3–9.0 mm	d 9.0 mm
Fig. a	Fig. b, c	Fig. d	Fig. f–h	Fig. i, j

1. nr. MNHN-F-A71902. – 20CS(14P,6TS), 2LS(P), 1R. – Figs. 7.3, 9a–j, 10.4a–d. [5 duplicate peels – nr. MB.K.8077].
2. nr. MNHN-F-A71904. – 11CS(5P,6TS), 2LS(TS),1R. – Figs. 7.6, 10.7a–b.
3. nr. MNHN-F-A71903. – 8CS(TS),1R. – Fig. 10.6.
4. nr. MB.K.8078. – 16CS/10P,6TS).3LS(TS). – Figs. 7.7, 10.1a–d.
5. nr. MB.K.8079. – 9CS(2P,7TS). – Fig. 7.4.
6. nr. MB.K.8080. – 7CS(TS). – Fig. 10.8a–b.

b) La Parisienne quarry, southern slope, Parisienne Member (term f) of the Ferques Formation, collection J.-C. Rohart 1977.

7. nr. MB.K.8081. – 12CS(2P,10TS). – Figs. 7.5, 10.5a–d.

c) La Parisienne quarry, islet at the eastern entrance, Parisienne Member (term f) of the Ferques Formation, collection D. LeMaître ca. 1960.

8. nr. MNHN-F-A71905. – 9CS(TS). – Figs. 7.2, 10.3a–b.

Diagnosis: Smaller long-conical *Metriophyllum* with only slighty shortened cardinal septum, archaeotheca without hyposeptal furrows.

Description: Small long-conical corals of 20–30 mm length (calicular diameter 9–15 mm), often slightly cornute (cardinal septum mostly at convex side), sometimes at base with a small talon. Archaeotheca with growth lines, longitudinal ribs and bifurcating septal furrows (schizosepta) indicating by their pinnate arrangement the positions of lateral septa and cardinal septum (Fig. 7.2). No additional furrows of hyposepta. Adult calice with 40–46 radially arranged septa starting near the calicular rim with a broader base. 19–22 major septa thin (leaving broader interseptal lumina), nearly of equal length, reaching the centre in the lower calice, there connected to form a small to medium-sized axial stereozone. Cardinal septum only slightly shortened in the upper and middle calice, then quickly growing to full length parallel with the closure of the fossular wall (Fig. 8h–k). The last major septum of every quadrant usually starts short like a minor septum; during later growth it causes temporary pinnate dispositions both in cardinal and counter quadrants (especially during early ontogenetic stages, Fig. 8b–d). Two counter minor septa longer, nearly reaching the length of major septa in adult stages, contratingent, since juvenile diameters of 2–3 mm forming a remarkanle triad with the counter septum. All other minor septa active only in the upper calice, disappearing in the middle calice by stereoplasmatic thickening of the archaeotheca (Fig. 10.5d). Metriophylloid carinae start in lower calicular phases and appear already in the early youth (Figs. 8a, 10.5a–b); they are arranged horizontally (not parallel to the upper margin of major septa, Fig. 10.1c) and often imitate minor septa. Tangential longitudinal sections (Fig. 9e) demonstrate varying positions on both sides of a major septum (at equal level or alternating). The central lumen of Fig. 10.1d is not an aulos, but indicates a starting amplexoid trend at maturity in the largest available specimen. Simple tabulae run steeply domed towards the axial stereozone. The cardinal fossula is only moderately deep and has no lateral thinning effect on the archaeotheca of everywhere equal thickness.

Metriophyllum columnare (Nicholson & Thomson, 1876)

Figs. 3.1a–c, 3.2, 6.1a–q, 6.2a–c, 11a–j, 12.3a–d, 12.4a–c

pars 1876 *Lindströmia columnaris*. – Nicholson & Thomson, p. 150.

pars 1878 *Lindströmia columnaris* Nich. and Thoms. – Nicholson & Etheridge, p. 84, fig. 4b', [non fig. 4b].

1900 *Lopholasma carinatum* (nom. propos.). – Simpson, p. 206, figs. 19–22.

pars 1945 *Metriophyllum rectum* (Hall). – Smith, p. 28, pls. 1, fig. 10 [non fig. 9], 34, fig. 2a–c [non fig. 3].

pars 1949 *Lindströmia columnaris* Nicholson and Thomson. – Stumm, p. 7, pl. 3, fig. 23 [non fig. 24]. [copied from Nicholson & Etheridge 1878].

1949 *Metriophyllum carinatum* Simpson. – Stumm, pp. 7, 60, pl. 3, figs. 8–10 [copied from Simpson 1900].

1964 *Metriophyllum carinatum* (Simpson 1900). – Holwill, p. 119, pl. 16, figs. 1–3.

pars 1981 *Lindstroemia columnaris* Nicholson & Thomson. – Hill, p. F201, fig. 122.3a [non 3b].

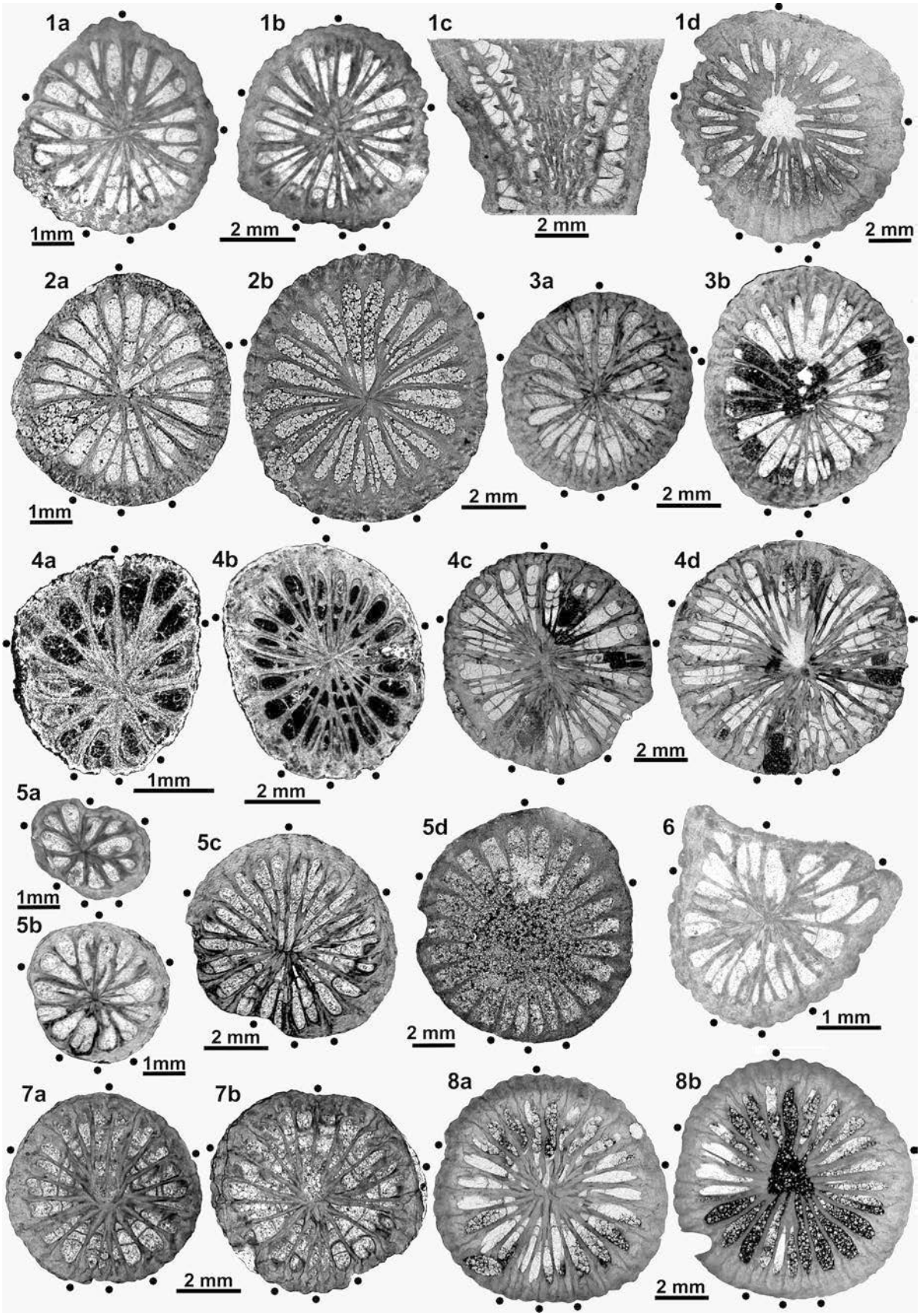
pars 1981 *Stereolasma rectum* (Hall). – Oliver & Sorauf, p. 103.

pars 1983 *Stereolasma rectum* (Hall). – Oliver & Sorauf, p. 47.

pars 1983 *Stereolasma* Association. – Brett et al., pp. 71, 84, 88.

Syntypes: Eight thin sections in the Henry Alleyne Nicholson (1844–1899) collections, Royal Scottish Museum, Edinburgh (catalogued by Benton, 1979), "Hamilton Formation, Erie, U.S.A.", commented by W.A. Oliver jr. (letter, 1986): "Erie is certainly the lake and refers to western New York" and "the type locality is certainly western New York and probably one of the Lake Erie shore sections in the upper half of the Hamilton Group, i.e. Ludlowville or Moscow Formation; however, there are innumerable sections in western New York that might have been termed Erie".

The map in Brett et al. (1983: 66) shows selected Hamiltonian coral localities over a distance of 160 km from Erie County to Seneca County (SE of Lake Erie und S of Lake Ontario), but only Erie County in westernmost New York State contacts Lake Erie and will be the "restricted" type locality, which still covers an area of 10–20 km and cannot be determined more precisely. This was the reason for an unpublished idea of W.A. Oliver jr. perhaps to prefer another lectotype designation for *Lindstroemia columnaris*: by choosing the longitudinal thin section (Nicholson & Etheridge 1878, fig. 4b; herein re-illustrated as Fig. 3.3a), the genus *Lindstroemia* Nicholson & Thomson, 1876 could become a nomen dubium for ever, because such an isolated longitudinal section is not determinable. Then, *Lopholasma* Simpson, 1900 with an exact type locality could be retained; this was not indicated in Simpson (1900: 206 – only "Hamilton shales, western New York"), but later improved by


1a
1b
1c
1d
1mm
2 mm
2 mm
2 mm
2a
2b
3a
3b
1mm
2 mm
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4b
4c
4d
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2 mm
2 mm
5a
5c
5d
6
1mm
2 mm
2 mm
1 mm
5b
1mm
7a
7b
8a
8b
2 mm
2 mm

Holwill (1964: 112 – "Hamilton Beds, Livonia salt shaft, Livingstone Co., N.Y."). We prefer another way and select a well determinable syntype, as both genera (*Lindstroemia*, *Lopholasma*) now fall definitely into the synonymy of *Metriophyllum*.

The eight syntypes (available for us only by photographs, not by the thin sections) comprise the three common Rugosa species abundant in the shaly Marcellus facies of the upper Hamilton Group (ahermatypic *Stereolasma* association): *Stereolasma rectum* (Hall, 1843), *Lopholasma carinatum* Simpson, 1900, *Amplexiphyllum hamiltoniae* (Hall, 1877), still united by Nicholson & Thomson (1876) in their new genus and new species *Lindstroemia columnaris*. Two of these thin sections were figured by Nicholson & Etheridge (1878: 84, fig. 4b, 4b'), being the base of all later interpretations/speculations about the genus *Lindstroemia* and its type species, and here copied in Fig. 3.1a, 3a (together with their first published photographs Fig. 3.1b, 3b, kindly provided by C.T. Scrutton in 1986). There are no doubts about the perfect identity between Figs. 1a, 1b and 3a, 3b, in spite of the slightly schematic drawings of 1878. The longitudinal thin section (Figs. 3a, 3b) had already been compared with *Stereolasma* Simpson, 1900 (without metriophylloid carinae – fig. 17 in Simpson 1900), e.g., by Stumm (1949: 7) and Neuman (1969: 55), but no transverse section exists to underline and verify finally such a generic assignment (in view of a still outstanding modern monograph of the Hamiltonian *Stereolasma* fauna, intended and started by W.A. Oliver jr.). The drawing of the transverse thin section from 1878 (Fig. 3.1a, 3.1b) is somewhat incorrect and did not allow to identify the protosepta and the antiseptal triad; they are found easily in the photographs, especially of an additional, hitherto unknown transverse section (Fig. 3.1c) prepared from the same specimen, which for sure is conspecific with *Lopholasma carinatum* Simpson, 1900.

Lectotype (designated herein): Specimen nr. 1968.15.41a. (figured by Nicholson & Etheridge 1878, fig. 4b') + nr. 1968.15.42d = 2 transverse thin sections (prepared from one coral), collection H.A. Nicholson, Royal Scottish Museum, Edinburgh – Fig. 3.1b, 3.1c.

Paralectotype: specimen nr. 1968.15.42b (Fig. 3.2) + nr. 1968.15.42c (not figured; coral broken into 5 fragments) = 2 thin sections (prepared from one coral), collection H.A. Nicholson, Royal Scottish Museum, Edinburgh.

Further material: Moscow Formation, Hamilton Group (middle Givetian); western New York State; donation W.A. Oliver jr. 1968.

Kashong Shale Member, Little Beards Creek, Moscow near Genesee, Livingston County:

1. Specimen nr. MB.K.8073 (old nr. SD5700/2) =17TS(14P,3TS),5LS(TS). – Figs. 11a–l. 12.3a–d.
2. Specimen nr. MB.K.8074 (old nr. SD5700/4) =18TS(13P,5TS),4LS(3P,1TS). – Figs. 6.1a–q, 12.4a–c.

Moscow Shale (lower part), Kidders NW of Ithaca, Seneca County.

3. Specimen nr. MB.K.8075 (old nr. SD5679/6) =7TS(P),6R. – Fig. 6.2a–c.

Diagnosis: Larger long-conical *Metriophyllum* (length 30 mm, calice diameter 15 mm, 50–55 major and minor septa), with hyposepta, strongly shortened cardinal septum.

Description: Our three well-preserved specimens of 21–30 mm length and 11–15 mm distal diameter are long-conical, straight (Fig. 12.3d) or very slightly cornute (Fig. 12.4a, cardinal septum in lateral position). Their archaeotheca bears narrow septal furrows of major and minor septa (schizosepta) in the typical tetracoralloid pinnate appearance and braod flat interseptal ribs (Fig. 6.1n) with intercalate weaker furrows of hyposepta (internally visible only at the uppermost calicular margin: Fig. 6.1o).

The primary calyx-ontogeny of the septal apparatus is shown by the serial sections of Figs. 6.1e–l, 11h–l. Septa start with a broad socket bearing a multitrabicular ornament of short granulations/spines (Fig. 6.1ln, o, q). Then major septa prolongate deeper in the calice as thin blades (with monacanth trabiculae, Fig. 6.1q), finally reaching – radially arranged – the centre, where they connect at first loosely, later forming a massive non-evert axial stereozone (Fig. 6.1e, 6.2b). They all are of more or less equal length, excepting the strongly shortened cardinal septum (reaching the centre later near the bottom of a slightly long-triangular fossula), and of course also excepting shorter growth phases of just new inserted major septa with temporary distinct pinnate appearance (well visible in early juvenile stages:

Fig. 10. *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850, topotypes, Ferques Formation (middle Frasnian), La Parisienne quarry east of Ferques (western face – Figs. 1, 2, 4, 6–8; eastern entrance – Fig. 3; southern slope – Fig. 5), collection D. LeMaître ca. 1960 (Fig. 5), J.-C. Rohart 1974 (Figs. 2, 4, 8) and 1977 (Fig. 5), J.-C. Rohart & D. Weyer 1993 (Figs. 1, 6, 7). **1a–d**. Specimen nr. MB.K.8078, Gris Member, subtabular transverse sections and eccentric longitudinal section, x8 (1a), x7 (1b), x5 (1c), x4 (1d). External photograph see Fig. 7.7. **2a–b**. Specimen nr. MNHN-F-A71901, neotype, Gris Member, subtabular and calicular transverse section, x8 (2a) and x6 (2b). External photograph see Fig. 7.1, for drawings see Fig. 8a–k. **3a–b**. Specimen nr. MNHN-F-A71905, Parisienne Member (term f), subtabular transverse sections, x6. External photograph see Fig. 7.2. **4a–d**. Specimen nr. MNHN-F-A71902, Gris Member, subtabular transverse sections, x15 (4a), x7 (4b) and x5 (4c, d). External photograph see Fig. 7.3, for drawings see Fig. 9a–j. **5a–d**. Specimen nr. MB.K.8081, Parisienne Member (term f), subtabular and calicular (5d) transverse sections, x8 (5a, b), x6 (5c) and x4 (5d). External photograph see Fig. 7.5. **6**. Specimen nr. MNHN-F-A71903, Gris Member, subtabular transverse section with fixing talon, x12. **7a–b**. Specimen nr. MNHN-F-A71904, Gris Member, subtabular transverse sections, x6. External photograph see Fig. 7.6. **8a–b**. Specimen nr. MB.K.8080, Gris Member, basal calicular transverse sections, x5.

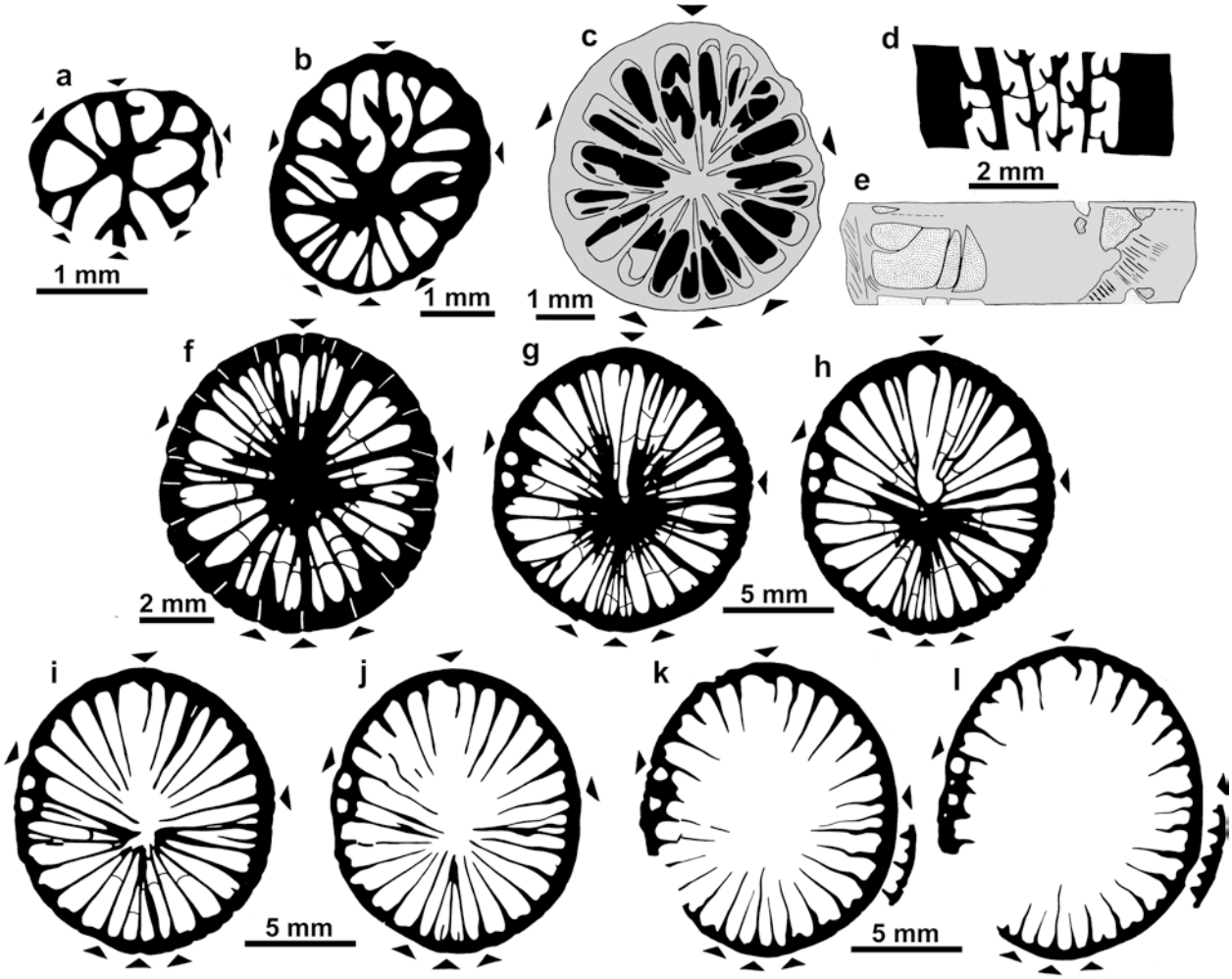

Fig. 11. *Metriophyllum columnare* (Nicholson & Thomson, 1876), Kashong Shale Member (Moscow Formation of Hamilton Group, middle Givetian), Little Beards Creek (= Moscow, near Genesee, New York), specimen nr. MB.K.8073, donation by W.A. Oliver jr. 1968. **a–c, f–l**. Series of transverse sections (nrs. 22, 19, 18, 13, 8–5, 3, 2, a–f subtabular, g–l calicular), x15 (a), x10 (b), x8 (c), x5 (f) and x3 (g–l). **d, e**. Tangential and median longitudinal section, x6. For photographs see Fig. 12.3a–d.

septal formulae:

2 I 2	3 I 3	3 I 3	4 I 5	5 I 5	5 I 5	5 I 6
3 I 3	4 I 4	5 I 5	7 I 5	7 I 6	8 I 7	8 I 7
n 14	n 18	n 20	n 25	n 27	n 29	n 30
N 20	N 28	N 33	N 42	N 46	N 50–51	N 52
d 1.7 mm	d 3.1 mm	d 4.9 mm	d 7.6x8.0 mm	d 11.7x12.7 mm	d 11.7x13.0 mm	d 12.0x14.0 mm
Fig. a	Fig. b	Fig. c	Fig. f	Fig. g	Fig. h–k	Fig. l

Figs. 6.1a, 11a–b). The course of the upper septal margin of major septa is shown by growth lines (Figs. 6.1p, 11e). Short minor septa are active in the upper calice and disappear later in the lower calice; this reduction sometimes follows a biform way (Fig. 11.h–j) – interior stereoplasmatic thickening of the archaeotheca starts in position I of an interseptal lumen (sensu Sutherland 1965) and appears later in position II. Only the two minor septa on either side of the counter septum grow longer and contratingent, building a remarkable triad starting already in the earliest stages (Fig. 11a).

Metriophylloid carinae appear below the middle calice (Figs. 6.1g, 11i–j) and are present in the observed most juvenile sections (Figs. 6.1a, 11a). Their course in longitudinal sections is horizontal, not parallel to the upper margin of

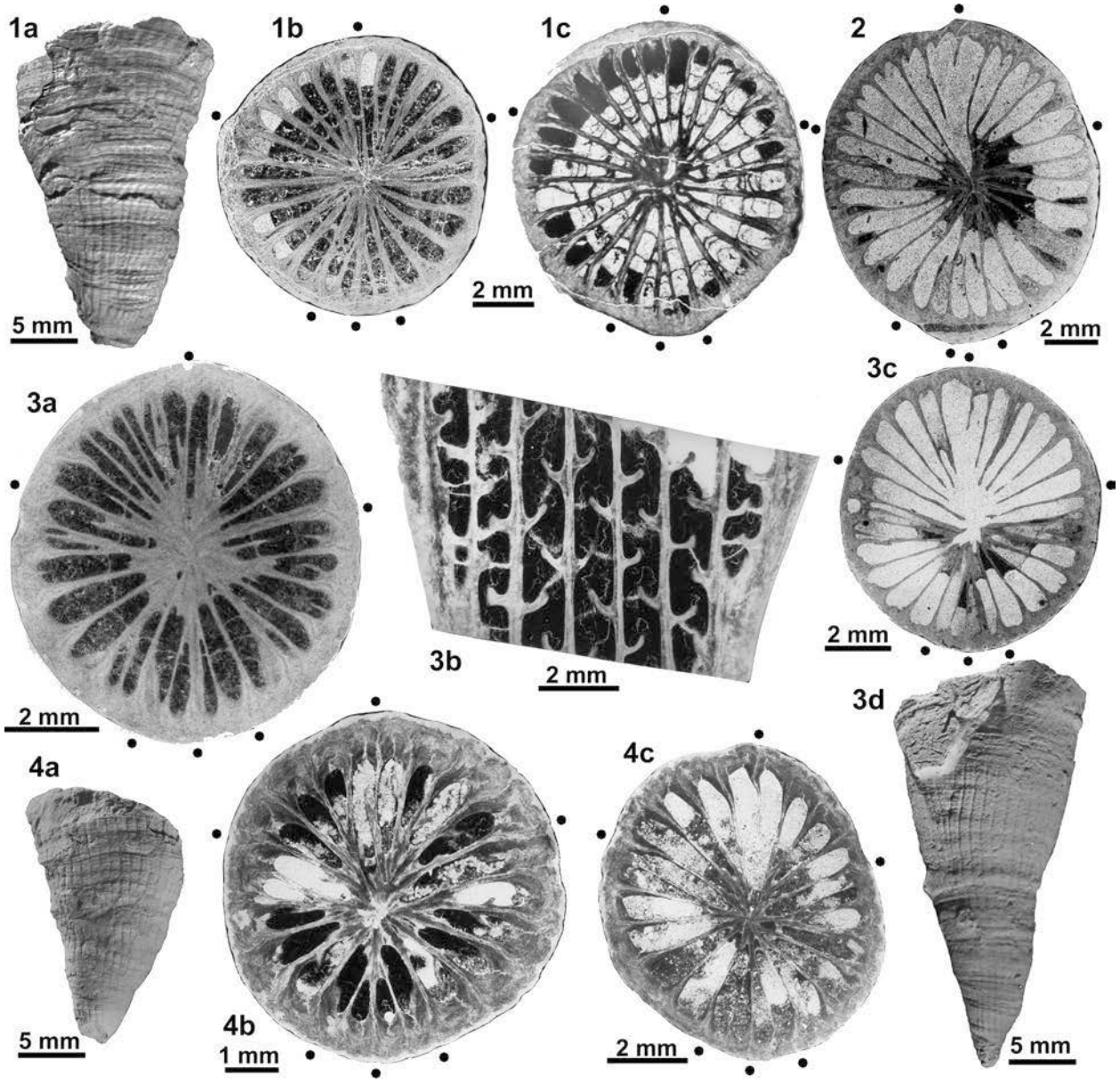

Fig. 12. Lindstroemiidae from the Givetian Hamilton Group of New York State (USA), donation of W.A. Oliver jr. 1968. **1–2**. *Stereolasma rectum* (Hall, 1843), Wanakah Shale member (Ludlowville Formation, lower Givetian), Athol Springs (5 miles S of Buffalo, near Lake Erie). 1. Specimen nr. MB.K.8071., a. External view of coral, x2. b, c. Transverse sections near the calicular base, x4.6 (b). Drawings see Fig. 5.1a–h. 2. Specimen nr. MB.K.8072, transverse section of lower calice, x4. Drawings see Fig. 5.2a–f. **3–4**. *Metriophyllum columnare* (Nicholson & Thomson, 1876), Kashong Shale Member (Moscow Formation, middle Givetian), Little Beards Creek (Moscow near Genesee). 3. Specimen nr. MB.K.8073. a. ubtabular adult transverse section, x7. b. Tangential longitudinal section just below calicular base, x8. c. Lower calicular transverse section, x5, d. External view of coral, x2. Drawings see Fig. 11a–l. 4. Specimen nr. MB.K.8074. a. External view of coral, x2. b, c. Lower calicular transverse sections, x8 (b) and x6 (c). Drawings see Fig. 6.1a–q.

major septa (Figs. 6.2b–c, 11e), and they are fixed either at the same level or alternating on both sides of a major septum. The number of these carinae varies: few in Fig. 3.1c, many in Fig. 6.2b. Well-preserved growth lines within the archaeotheca always allow a clear distinction between minor septa (hidden in the wall) and carinae. The simple tabulae are strongly domed; tabellae were not observed in the few prepared longitudinal sections.

Fig. 11a is the earliest available stage of the secondary postcalyx-ontogeny, with seemingly 12 visible septa, but in reality 20 septa (6 protosepta, 8 metasepta, 6 catasepta) – hidden within the wall are 4 catasepta and 4 metasepta. The juvenile growth phases of Fig. 6.1a–b are characterized by a somewhat stronger stereoplasmatic thickening of septa and narrower interseptal lumina. The aseptal larval stage (prototheca) was not preserved.

Remarks: The two transverse sections of the lectotype are well comparable (in size and septal numbers) with the specimen of Fig. 11. Their compact axial stereozone had been misinterpreted in 1876 as a pseudocolumella; therefore *Lindstroemia* Nicholson & Thomson, 1876 was thought for a certain time to be a columellate coral – as based on the Wenlockian *Dalmanophyllum dalmani* (Milne-Edwards & Haime, 1851) in Nicholson & Etheridge (1878). But such a taxon with an axial boss has never been described among the ahermatypic Rugosa community of the upper Hamilton Group, though such genera occur in other Middle Devonian coral faunas (*Hamaraxonia* Berkowski & Weyer, 2012, Eifelian of Morocco; *Cyathaxonia*? *hercynica* Roemer, 1855, Givetian of Germany, France and Morocco – Weyer & Zagora 1990, fig. 3, representing a new genus: Weyer & Berkowski, in preparation). A series of narrow situated transverse sections in the lower calice (as in Fig. 6.1g–i) demonstrates that there exist no everted septal lamellae at the axial ends of major septa and no everted median lamella of counter-septal origin, which usually construct a pseudocolumella.

The synonymy includes faunal list citations of *Stereolasma rectum* (Brett et al. 1983; Oliver & Sorauf 1983); these authors followed W.A. Oliver jr., at that time accepting *Lopholasma carinatum* and *Stereolasma rectum* as one species (as declared by Smith 1945). He "warned" D. Weyer in discussions (1991, Münster coral congress) not to overestimate the taxonomic value of metriophylloid carinae; we do not know if he maintained this opinion during his started, but up to his death in 2005 unfinished and unpublished studies for a monographic revision of the Hamiltonian (Givetian) *Stereolasma* association. Our restricted materials of such Rugosa from western New York State (Figs. 4, 5, 6, 11, 12) demonstrate a second distinguishing feature between *Lopholasma* and *Stereolasma* (reduced or contratingent minor septa). Thus we keep the two genera as separate taxa, but perhaps this conception might be disproved by the only transverse section of *Lopholasma carinatum* in Simpson (1900, fig. 19), where that author had drawn contratingent minor septa. Photographs of the same transverse section (Smith 1945, pl. 3, fig. 10; Holwill 1964, pl. 16, fig. 2) seem to support the presence of active contratingent minor septa, not always easy to distinguish from metriophylloid carinae (as in Fig. 6.2a). This open question underlines the need of intensive morphological revisions of *Metriophyllum* and *Stereolasma* throughout their complete life span within the Hamilton Group (Fig. 4).

Comparisons: The species differs from *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850 by its larger size (connected with a higher number of septa), the much more shortened cardinal septum, and the presence of hyposepta (at present not recorded from any further *Metriophyllum*). The latter feature is shared in identical manner with *Stereolasma rectum* (Hall, 1843) (compare Weyer 1997, pl. 1, figs. 2–3), arousing the problematical suspicion of genetic relationships.

Acknowledgements

W.A. Oliver jr. (1926–2005) donated 1968 (then Washington) Hamiltonian corals for comparison purposes and discussed (1981, 1986, 1991) the morphological and taxonomical problems around *Lindstroemia*, *Lopholasma* and *Stereolasma*. C.T. Scrutton (then Newcastle-upon-Tyne) provided 1986 the photographs of all syntypes of *Lindstroemia columnaris* Nicholson & Thomson, 1876 from the Royal Scottish Museum in Edinburgh and commented their classification. In 2008, C.E. Brett (Cincinnati) loaned his collection of Rugosa from the Givetian Tully Limestone of New York State. J.G. Darrell (London) informed in 2019 about the *Metriophyllum* collections from Ferques (Boulonnais) stored in the British Museum of Natural History. J.-M. Pacaud (Paris) confirmed in 2019 the loss of the *Metriophyllum bouchardi* Milne-Edwards & Haime, 1850 syntypes in the Musée National d'Histoire Naturelle, thus allowing us to propose a neotype. A. Ehling (Berlin) always loaned necessary coral materials from the Bundesanstalt für Geologie und Rohstoffe (Außenstelle Berlin – collections of the former Preussische Geologische Landesanstalt and Zentrales Geologisches Institut). Yu Chang-Min (Nanjing) translated some Chinese literature and reviewed the manuscript. An intensive review was also provided by J. Fedorowski (Poznań). We thank them all for their kind help.

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