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Rugose corals across the Early-Middle Devonian boundary in southern Belgium

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Abstract

In southern Belgium, the Emsian-Eifelian Boundary falls within the uppermost part of Moulin de la Foulerie Formation (Eau Noire Member), and is overlain by the lower Eifelian Couvin Formation (Villers-la-Tour and Petigny members). The Emsian part of the Eau Noire Member mostly comprises bioclastic limestone and calc-shale alternations whereas the Eifelian part consists of coral-stromatoporoid biostromes and siltstone. All these units are relatively rich in macrofauna, including locally abundant rugose corals. The taxonomic revision of the rugose coral collected below and above the boundary led to the identification of 28 species in 19 genera. Coral species previously described by H.H. Tsien are here re-described and their diagnoses are amended. The Emsian coral fauna is almost entirely composed of large solitary corals dominated by species of *Acanthophyllum* and *Nardophyllum*, associated with *Calceola, Digonophyllum, Mesophyllum,* and *Tabulophyllum* as well as the smaller corals *Kunthia, Stringophyllum,* and putative *Chostophyllum; Microplasma* is the only colonial genus recorded in the upper part of the Eau Noire Member. Undissepimented solitary corals are represented by *Adradosia*, *Metriophyllum* and *Neaxon*. The lower Eifelian yields *Digonophyllum, Grypophyllum, Lekanophyllum, Nardophyllum,* and *Zonophyllum,* as well as *Adradosia* and the colonial *Sociophyllum*. A new species of *Sociophyllum* is described from the basal Villers-la-Tour Member. No significant faunal change occurs across the Lower-Middle Devonian boundary, but the extinction of *Tabulophyllum lissingenensis* and *Nardophyllum originale* is located at the base of *partitus* conodont Zone. The coral association is similar in the Ardennes and Eifel Hills, though differences exist. Emsian coral assemblages from Brittany, the Cantabrian Mountains, the Montagne Noire and the Carnic Alps are very different, notably with the occurrences of colonial genera and endemic taxa.

Keywords Cnidarian · Emsian · Eifelian · Couvinian · Stratigraphy · Diversification

Introduction

Along the southern margin of the continent Laurussia, sedimentation switched from siliciclastic to carbonate at the end of the Emsian stage (Early Devonian), due to climate change and the reduction of erosion on lands. With this change of facies, the benthic community started to diversify, with the onset of rugose and tabulate corals as well as stromatoporoids, announcing the development of the Middle Devonian diverse reefal environment.

In the Namur-Dinant Basin of southern Belgium, these changes of fauna and facies were traditionally used to define the lower boundary of the 'Couvinian' disused regional stage (Lecompte 1955), notably with the entry of *Calceola sandalina* and *Arduspirifer intermedius*. To document the biostratigraphy of the 'Couvinian', Marius Lecompte, an eminent Belgian palaeontologist supervised three PhD theses: the brachiopods were analysed by Godefroid (1968), the rugose corals by Tsien (1969) and the conodonts by Bultynck (1970). These monographic works established the subdivision and correlation of the 'Couvinian' based on assemblages defined among the three fossil groups.

Between 1973 and 1981, the International Subcommission for Devonian Stratigraphy discussed the definition of the base of the Middle Devonian. Four potential conodont-based horizons

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were proposed: the base of the *Polygnathus dehiscens* Zone, the base of the *P. patulus* Zone, the base of the *P. partitus* Zone, and the base of the *P. costatus* Zone. The second criterion was coincident with the base of the 'Couvinian' stage whereas the third was almost coincident with the base of the Eifelian stage. In 1980, the voting members of the Subcommission voted for the base of the *P. partitus* Zone which, once ratified in 1981, became the base of the Middle Devonian with the Eifelian retained as the official name for its lower stage (Ziegler and Klapper 1982). The GSSP was chosen in the Wetteldorf Richtschnitt section in the Eifel Hills, in Germany, with the entry of the conodont *P. partitus* in bed n°30, 1.9 m below the boundary between the Heisdorf and Lauch Formations (Ziegler 2000).

For the establishment of the GSSP in the Wetteldorf Richtschnitt section, the stratigraphic distribution of the rugose corals was examined by Birenheide (in Werner and Ziegler 1982). Faunal lists were provided but few corals were described or figured (except for some type material from Wedekind's collection published by Birenheide (1978, 1979)). In the Belgian sections, Tsien (1969) described 40 species of rugose corals from the Moulin de la Foulerie Formation and the basal part of the Couvin Formation. Tsien's systematic work was conducted on poorly preserved, fragmentary material and was in need of revision. Based on Tsien's specimens, and newly collected material, the rugose corals across the Emsian-Eifelian boundary are here revised.

Geological settings and stratigraphy

The Dinant Synclinorium, a wide structure belonging to the Variscan fold-and-thrust belt, exposes the sedimentary succession of the Emsian-Eifelian along its northern and southern margins (Fig. 1). Along the northern to north-eastern margin, the succession is lacunar and corresponds to the deposition of typical Old Red Sandstone facies. Along the southern margin, on the contrary, the succession is entirely marine and the Emsian-Eifelian strata reach several hundreds of metres in thickness. Sections exposing the fossiliferous upper Emsian and lower Eifelian are situated between Chimay and Marche-en-Famenne (Fig. 1). The sampled outcrops and sections are given in Appendix 1.

The Moulin de la Foulerie Formation is a new term recently introduced by the Belgian Subcommission on Devonian Stratigraphy consists of two units, previously described as formations but nowadays considered members: the Saint-Joseph Member and Eau Noire Member (Denayer and Mottequin 2024). These two names were originally introduced by Tsien (1974) as the two members of the Bure formation but the latter formation was dismissed by Bultynck and Godefroid (1974) as no continuous section is available in the type locality. In the classical Belgian literature, the formation is referred to the 'Coa' (*sensu* Conseil de Direction de la Carte géologique de Belgique 1892). The Saint-Joseph Member corresponds to the 'Co1a'

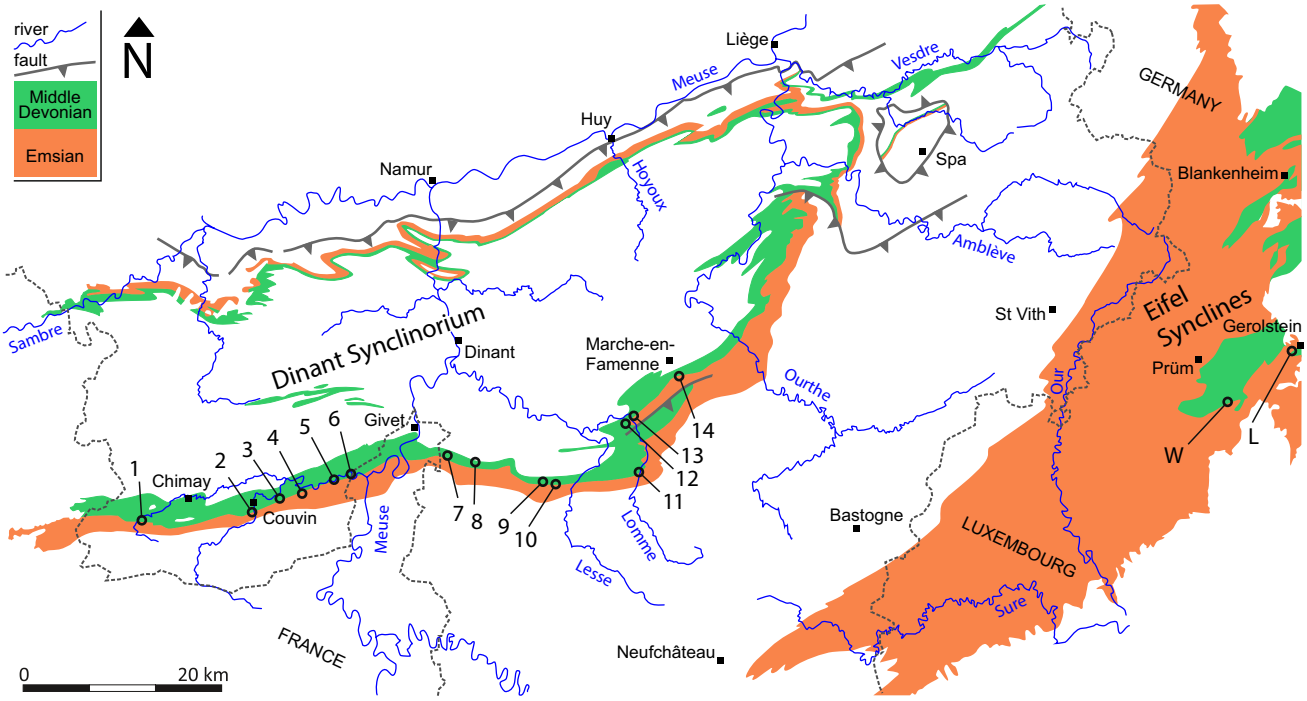

Fig. 1 Simplified geological map of the Ardennes and Eifel Hills, with location of the sampled sections: *1* Villers-la-Tour, *2* Couvin, Eau Noire River, *3* Petigny and Cul d'Efer, *4* Olloy, *5* Treignes, *6*: Najauge and 'Mur des Douaniers', *7* Dion, *8* Wancennes, *9* Sohier, *10* Halma, *11* Grupont, *12* Jemelle railway, *13* Jemelle station, *14* Waha, *L* Lissingen, *W* Wetteldorf. See Appendix 1 for details

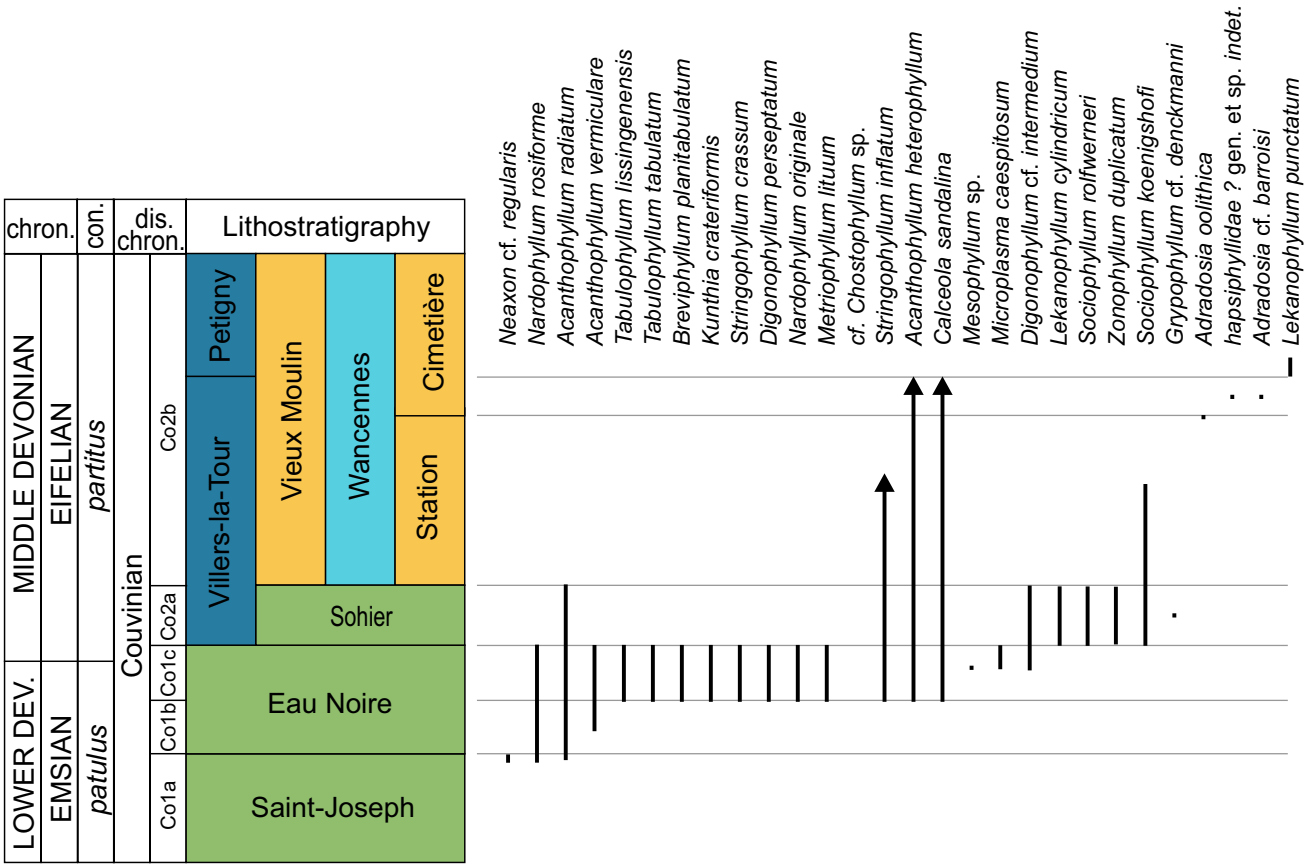

Fig. 2 Simplified chrono- and lithostratigraphic chart with the extension of the rugose coral species described herein. Legend: *chron*. chronostratigraphy, *con*. conodont standard zones, *dis. chron*. disused chronostratigraphic units (see main text); *Dark blue units* Villers-la-Tour and Petigny Members of the Couvin Formation, *green units* Saint-Joseph and Eau Noire Members and Sohier Beds of the Moulin de la Foulerie Formation, *yellow units* Vieux Moulin, Station and Cimetière Members of the Jemelle Formation

whereas the Eau Noire Member is referred to as the 'Co1b-c' (*sensu* Maillieux 1912) (Fig. 2).

The Saint-Joseph Member is characterised by its increasing carbonate content following the Lower Devonian siliciclastic succession. It is mostly made of fossiliferous siltstone and sandstone with impure bioclastic limestone beds containing a marine fauna dominated by crinoids and brachiopods, notably *Paraspirifer cultrijugatus, Alatiformia alatiformis* and *Glossinulus mimicus* (Godefroid 1968). Corals are neither abundant nor diverse. *Favosites* sp. and small rugose corals such as *Adradosia* spp. are known from the lower part of the formation (including in the basal haematitic bed, Fig. 3a) but most of the fossils are known as steinkerns (decalcified internal moulds). Calcitic fossils are only known from the upper part and are represented by small undissepimented rugose corals, rare cystimorphic rugosa and *Acanthophyllum* spp. and small colonies of *Favosites* sp. Mistiaen (2007) mentioned a single stromatoporoid collected in the lower part of the Saint-Joseph Member.

The Eau Noire Member is composed of bioclastic calc-shale and calc-siltstone rich in crinoids, brachiopods, bryozoans and corals (Fig. 3b). Thin limestone beds and nodules occur in the lower half whereas the upper half is dominated by cyclic alternations of crinoidal calc-shale and argillaceous limestone. Brachiopods are particularly abundant, *Paraspirifer cultrijugatus, Zdimir hercynicus, Uncinulus orbignyanus* and *Atrypa reticularis* are the typical markers (Godefroid 1968). Corals are uncommon and usually fragmented in the lower part of the Eau Noire Member, except small hemispherical colonies of *Favosites* sp. and poorly preserved *Calceola sandalina*. The upper two thirds of the member, conversely, are very rich and the fauna is diverse and most of the coral specimens described here come from this part (Fig. 4).

The uppermost 4 or 5 metres of the Moulin de la Foulerie Formation are composed of thickly-bedded finely bioclastic limestone described by Denayer and Mottequin (2024) as the Sohier Beds, a laterally very continuous marker level corresponding to Maillieux's (1912) 'Co2a'. These beds yielded almost no rugose corals and only alveolitid tabulate corals.

The Emsian-Eifelian Boundary–and therefore the Early-Middle Devonian Boundary–falls within the uppermost part of the Eau Noire Member of the Moulin de la Foulerie

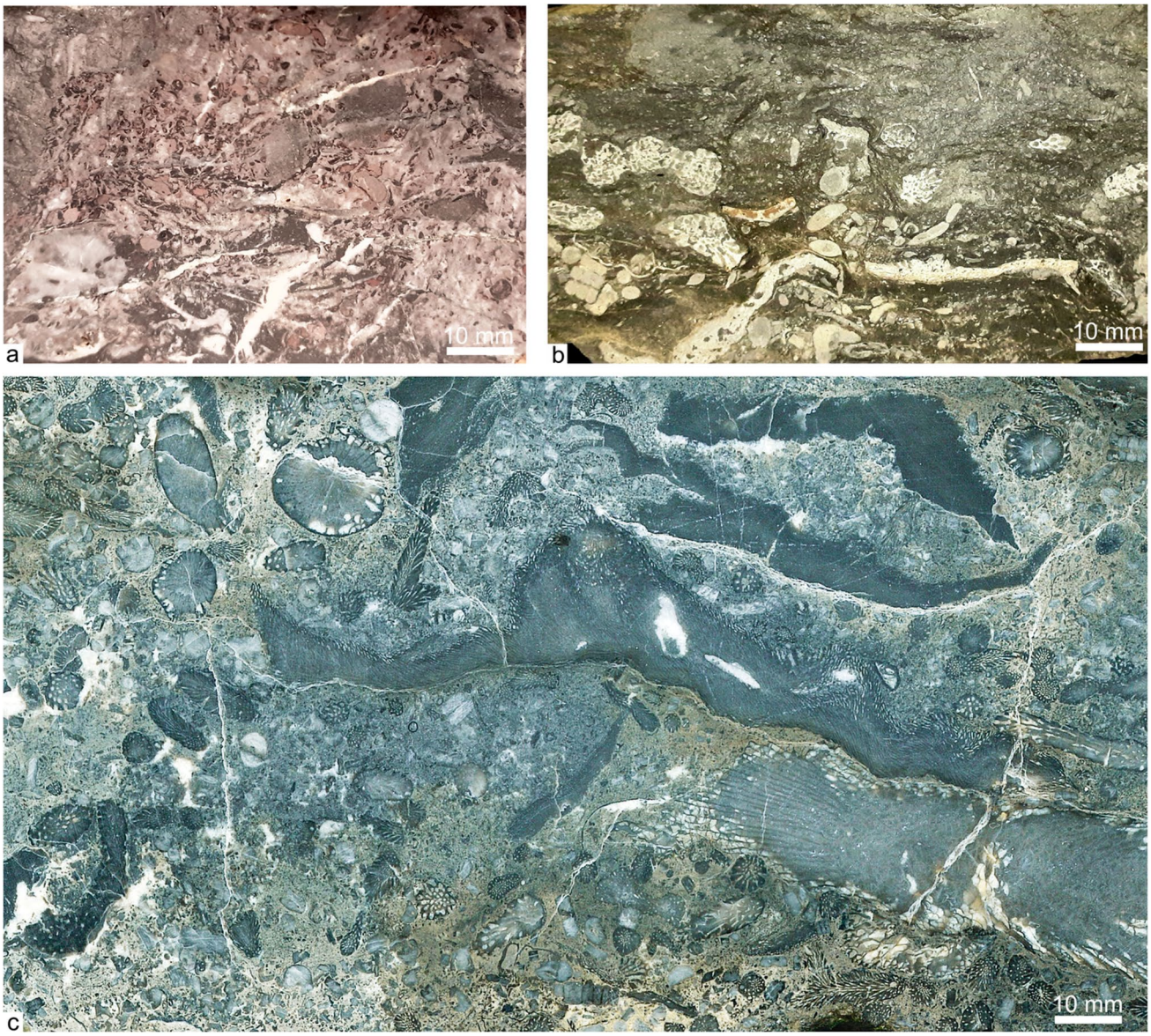

Fig. 3 Selected facies of the Emsian-Eifelian succession. **a** Horizon with haematitized bioclasts and haematitic oolites (*Adradosia oolithica* in the bottom left corner), from the base of the Saint-Joseph Member, Waha section, polished slab, W-II/2. **b** Bioclastic argillaceous limestone with tabulate corals, upper part of the Eau Noire Member, Halma section, acid-etched polish slab, WZH-II/22. **c** Tabulate coral and stromatoporoid biostrome with *Sociophyllum koenigshofi* sp. nov., Villers-la-Tour Member, Villers-la-Tour section, polished slab VTR-I/18

Formation which lower boundary was the traditional base of the disused 'Couvinian' stage (Fig. 2). In the Eau Noire River section, the first appearance of *Icriodus retrodepressus* in bed n°54, 5 m below the top of the Eau Noire Member indicates the base of the *partitus* Zone and therefore the base of the Eifelian stage (Bultynck and Godefroid 1974). In the Saint-Joseph section, this first appearance falls in a thin limestone bed c. 11 m below the top of the Eau Noire Member (Bultynck et al. 2000). A single specimen of *P. partitus* is reported from a bed situated 4 m below the top of the Eau Noire Member in the Grupont section (Godefroid 1968). Consequently, most of the fauna is the Eau Noire Member is still Emsian in age.

The Couvin Formation, in its stratotype, along the Eau Noire River, starts above the last thick bed of calc-shale of the Moulin de la Foulerie Formation (Fig. 2). Its lower unit, the Villers-la-Tour Member is composed of crinoidal and bioclastic limestone rich in stromatoporoids and massive tabulate corals that form biostromes (Fig. 3c). The corals are abundant but poorly diverse. The first colonies of *Sociophyllum* appear c.

10 m above the base in the Villers-la-Tour section. The second unit, Petigny Member (Denayer 2019) is composed of fine-grained black limestone with shaly and nodular intercalations. A very peculiar fauna of pelecypods and ostracods is found in this facies, suggesting dysoxic conditions that were interpreted by Denayer (2019, 2023) as the effect of the Choteč event and the maximum flooding interval of the third-order eustatic sequence MD1. Corals are very rare in this member and only *Lekanophyllum punctatum* is recorded with small colonies of *Favosites* sp. and alveolitids. A third member, the Cul d'Efer Member is also composed of biostromes but is not taken into account in the present paper. These three members were previously designated under the names 'Co2a-b' (Maillieux 1912), and Foulerie member (Bultynck et al. 1991).

The Couvin Formation corresponds to the lower part of the Eifelian between Glageon (France) and Nismes, east of Couvin. Eastwards, the lower three members of the Couvin Formation are replaced by a thick unit of fine-grained siliciclastics named Vieux Moulin Member of the Jemelle Formation (Dumoulin et al. 2006). This member starts above the Sohier Beds (uppermost part of the Eau Noire Member), with dark siltstone and shale beds yielding only decalcified fossils, including the renowned trilobites of the 'Mur des Douaniers' locality at the Belgium-French border (e.g. Crônier and Van Viersen 2008). Corals are rare in these facies and appear usually as external moulds. The upper part of the member contains a dark sandstone unit that yielded very few fossils, including small undissepimented rugose corals. The Vieux Moulin Member passes, east of Wellin, to two members, namely the Station Member (siltstone and shale with some sandstone horizons) and the overlying Cimetière Member (siltstone and shale with nodular limestone). The first is very poor in fauna, but the second yields a diverse brachiopod fauna, including the marker *Arduspirifer intermedius* (see Godefroid 1968), and rare undissepimented rugose corals.

The Wancennes Formation is a lenticular biohermal limestone unit resting on the top of the Moulin de la Foulerie Formation. Its base is composed of crinoidal and bioclastic limestone alternating with coral-stromatoporoid biostromes (Denayer 2023). The lower part yielded a coral fauna very similar to that known at the base of the Couvin Formation.

Systematic palaeontology

Beside the type material of Tsien's collection, curated at the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) and Wedekind's and Birenheide's collections in the Senckenberg Forschungsinstitut (Frankfurt, Germany), all the material is deposited in the Animal and Human Palaeontology collections of the Université de Liège (Belgium).

The suprageneric classification follows Hill (1981). The systematics of cystimorphic corals follows Pedder and McLean (1982) emended by McLean (2021). Their detailed argumentation for the use of the generic names *Nardophyllum, Zonophyllum* and *Microplasma* within the Cystiphyllinae and *Digonophyllum* and *Lekanophyllum* within the Digonophyllinae is not repeated here. The morphological terms are from Hill (1981) and McLean and Pedder (1976). The synonymy lists are established following Matthews (1973).

Order Stauriida Verrill, 1865
Family Endophyllidae Torley, 1933
Genus *Tabulophyllum* Fenton and Fenton, 1924

Type species: *Tabulophyllum rectum* Fenton and Fenton, 1924, from the Frasnian of Iowa.
Diagnosis: See Sorauf (1998).
Discussion: Historically (e.g. Hill 1942a), *Tabulophyllum* Fenton and Fenton, 1924 was supposedly restricted to the Middle-Late Devonian and older species were referred to *Sinospongophyllum* Yoh, 1937 only on an age basis. Subsequent workers considered that *Sinospongophyllum* is not sufficiently different to be separated from *Tabulophyllum*. For Stumm (1949), only the development of minor septa differentiates the two genera. For Shen (1995), they differ by the development of the stereoplasma in the dissepimentarium. Such differences are purely within the range of intraspecific variation. Hence, following Hill (1981) and Sorauf (1989, 1998), *Sinospongophyllum* is regarded as a junior synonym of *Tabulophyllum*.

Papiliophyllum Stumm, 1937 is relatively similar to *Tabulophyllum* but differs in having a deep cardinal fossula and lacking septal crests on the lonsdaleoid dissepiments (Pedder and Murphy 2003). These genera are homeomorphic but their distinct origin and suprageneric classification can be assessed by the microstructure of the septa: Papiliophyllidae with coarse monacanthine trabeculae (Pedder and Murphy 2003), Kyphophyllidae with very fine monacanthine trabeculae (Sorauf 1989, 1997). Birenheide's (1974) attribution of Emsian corals to *Papiliophyllum* was poorly constrained and Schröder (2002) then Pedder and Murphy (2003) reattributed those specimens to *Tabulophyllum* based on the characters cited above.

Tabulophyllum lissingenensis (Birenheide, 1974)
(Figs 4c, 6a–j, 7a–b)

1969 *Tabulophyllum multiseptatum*; Tsien, p. 39, pl. 6, fig. 1a–e, pl. 52, fig. 4
1969 *Tabulophyllum conicum* (Wang, 1948); Tsien, p. 39, pl. 6, fig. 2a–b
1969 *Tabulophyllum formosum* Tsien, p. 40, pl. 6, fig. 3a–d, pl. 49, fig. 1a–e
*1974 *Papiliophyllum lissingenense*; Birenheide, p. 253, fig. 1


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◂**Fig. 4** Morphologies of selected corals from the Eau Noire Member. **a** Scolecoid *Acanthophyllum vermiculare*, specimen W/47, Waha section. **b** Conical *Nardophyllum rossiforme*, W/48, Waha section. **c** Trochoid *Tabulophyllum lissingenensis*, W/49, Waha section. **d** Cylindrical *Acanthophyllum vermiculare*, W/50, Waha section. **e** Cylindrical *Acanthophyllum heterophyllum*, WZH/14, Halma section. **f** Trochoid *Acanthophyllum radiatum*, W/51, Waha section. **g** Ceratoid *Adradosia oolithica*, VIR/1, 'Mur des Douanier', Vieux Moulin Member. **h** Scolecoid *Tabulophyllum tabulatum* covered by platy alveolitid, W/52, Waha section. **i** Cylindrical *Stringophyllum inflatum*, WZH-II/24, Halma section. **j** Fasciculate *Microplasma caespitosum*, WZH-II/1, Halma section. **k** Budding *Microplasma caespitosum*, WZH-II/2, Halma section. **l** Patulate *Kunthia crateriformis*, CBR/2, Couvin section. **m** Trochoid juvenile *Acanthophyllum heterophyllum*, W/53, Waha section. **n** Slender cylindrical *Stringophyllum crassum*, WZH-II/23, Halma section. **o** Scolecoid *Nardophyllum rossiforme*, JG-IB/8, Jemelle station section. **p** Small scolecoid *Zonophyllum duplicatum*, JG-IB/9, Jemelle station section

1977 *Tabulophyllum multiseptatum* Tsien, 1969; Tsien, p. 268, fig. 3

1978 *Papiliophyllum lissingenense* Birenheide; Birenheide, p. 67, pl. 9, fig 1

Remarks: When establishing the new species *P. lissingenense* [sic] based on Emsian material from Lissingen, Birenheide (1974) apparently ignored Tsien's publication issued several years earlier. However, Tsien's (1969) species were cited only once, by Tsien (1977), who also ignored Birenheide's (1974) species! Although the generic attribution is incorrect, the German species was abundantly cited during the last 50 years, making consequently *T. multiseptatum* and *T. formosum* two *nomina oblita*. Hence, following the ICZN, *T. lissingenensis* (Birenheide, 1974) is the retained correct name.

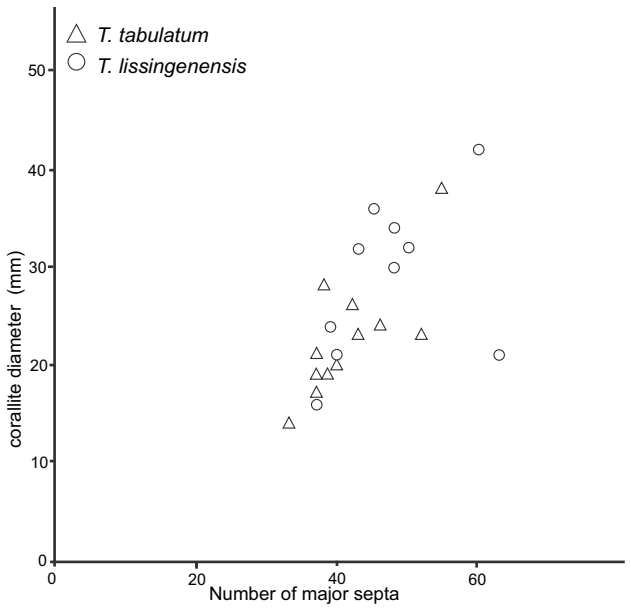


Fig. 5 Corallite diameter plotted against the number of major septa for the species *Tabulophyllum lissingenensis* and *T. tabulatum*

Holotype: SMF 30051, figured in Birenheide (1974, pl. 1, fig. 1a–c).

Material: Eight coralla from the Eau Noire Member (three specimens from the Jemelle-station section, one from the Eau Noire River section, three from Waha, and one from Halma). Additionally, the type specimen of *T. multiseptatum* (n°1551) from the Eau Noire River section is missing from Tsien's collection in the Royal Belgian Institute of Natural Sciences but the type specimen of *T. formosum* (n°1075) is here studied and photographically figured for the first time.

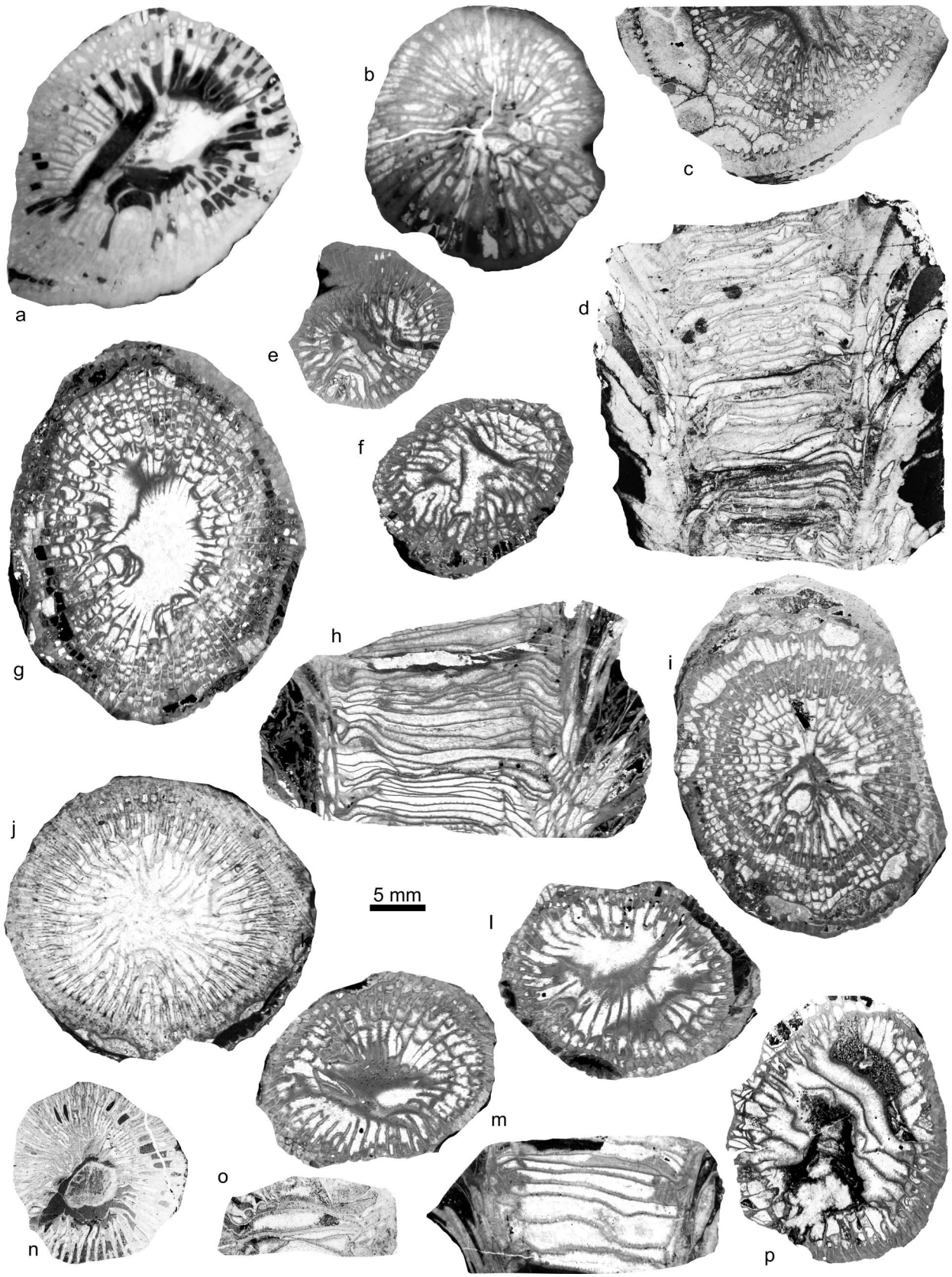
Type locality and horizon: Lissingen, Eifel Hills, upper Emsian Heisdorf Formation (Birenheide1974).

Diagnosis (emended from Birenheide 1974): Solitary coral up to 30 mm in diameter, having up to 46 septa of each order, with dissepiments at all growth stages, wide tabularium with 6–10 tabellae per vertical centimetre.

Description: Solitary trochoid to cerato-cylindrical coral with calicular expansions and constrictions, 20–30 mm in diameter, with a tabularium 20–25 mm in diameter in mature stages, and having up to 60 septa of each order (Fig. 5). All septa thin in dissepimentarium and tabularium, with sharp ends. Base of the septa embedded in the wall or appearing as septal crests on lonsdaleoid dissepiments (Figs 6e, i). Major septa long but withdrawn from the axis, leaving an empty space up to 20 mm in diameter (Fig. 6g). Cardinal major septum shorter, cardinal lateral septa bent towards the cardinal fossula (Fig. 6j). Minor septa long, reaching the margin of the tabularium, more discontinuous than the major septa (Fig. 7a). Dissepimentarium made of 1–4 rows of large lonsdaleoid dissepiments covered with stereoplasma (Figs 6c, j), and 4–10 rows of small concentric dissepiments, several rows being thickened (Fig. 6e). In longitudinal section, dissepiments 5–10 mm long, 1–2 mm high, inclined at 70–90° towards the tabularium (Fig. 7b). Tabularium wide, made of complete tabulae, flat to mesa-shaped with a peripheral gutter (Figs 6d, h), regularly spaced (8–14 tabulae per vertical centimetre). Wall up to 1.1 mm thick, slightly undulating.

Discussion: Both topotypes of *T. multiseptatum* Tsien, 1969 from the Eau Noire River section and other specimens share the typical characteristics of *T. lissingenensis* as defined by Birenheide (1974): wide tabularium with relatively flat tabulae, large lonsdaleoid dissepiments interrupting the septa at all growth stages, numerous slender septa. The attribution of this species to *Papiliophyllum* by Birenheide (1974) is contested as the German specimens lack the septal thickening of the typical Papiliophyllidae (Sorauf 1998; Schröder 2002; Pedder and Murphy 2003).

Tabulophyllum formosum Tsien, 1969, found in the same beds was described as smaller and having less and smaller septa. However, Tsien's collection is rather limited and it appears that the holotype of *T. formosum* is only a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◂**Fig. 6** **a–j** *Tabulophyllum lissingenensis* (Birenheide, 1974), from the Eau Noire Member. **a–b** Holotype of *Papiliophyllum lissingenense* Birenheide, 1974, from the Lauch Formation, Lissingen section, thin sections 30051-52 (Senckenberg Forschungsinstitut, coll. Birenheide), in transverse section (TS). **c–d** Holotype of *Tabulophyllum formosum* Tsien, 1969, from the Eau Noire Member, specimen 3068 (IRSNB, coll. Tsien), Eau Noire River section, c in TS, d in longitudinal section (LS). **e–h** Specimen JG-II-F/1, Jemelle station section, **e–g** successive TS, h in LS. **i** Specimen CEN-B/3, from the Eau Noire River section, in TS. **j** Specimen WZH/25, Halma section. **k–p** *Tabulophyllum tabulatum* Tsien, 1969 from the Eau Noire Member. **k–m** Specimen W/16, Waha section, k–l in TS, m in LS. **n–o** Holotype of *Tabulophyllum tabulatum*, specimen 3061 (IRSNB, coll. Tsien), Eau Noire River section, n in TS, o in LS. **p** W/7, Waha section, TS

sub-mature specimen of *T. lissingenensis* (Birenheide, 1974).

Distribution: *Tabulophyllum lissingenensis* is known from the uppermost part of the Heisdorf Formation (Birenheide 1974) and the uppermost part of the Eau Noire Formation, both in the upper part of the Emsian *patulus* Zone, immediately below the base of the Eifelian. Up to now, the species has not been reported outside the Eifel Hills and the Ardennes, except for a species assigned to *Papiliophyllum multiseptatum* (Tsien, 1969) by Soto (1984) in a faunal list of the Moniello Formation of the Cantabrian Mountains.

Tabulophyllum tabulatum Tsien, 1969
(Figs 4h, 6k–p)

* 1969 *Tabulophyllum tabulatum*; Tsien, p. 41, pl. 22, fig. 3–7, pl. 49, fig. 2–5
1969 *Tabulophyllum firmatum*; Tsien, p. 41, pl. 5, fig. 1–3
? 1969 *Breviphyllum dilatatum*; Tsien, p. 50, pl. 49, fig. 6a–b

Holotype: Specimen 3061 figured in Tsien (1969, pl. 49, fig. 5a–b).

Material: Fourteen coralla from the Eau Noire Member (seven specimens from the Waha section, six from Halma and one from Grupont). Additionally, the type specimen n° 3061 from the Eau Noire River section was studied. The type specimen of *T. firmatum* (n° 1100) from the Eau Noire River section is missing from Tsien's collection.

Type locality and horizon: Section on the left bank of the Eau Noire River in Couvin, upper part of the upper Emsian Eau Noire Member ('Co1c') (Tsien 1969).

Diagnosis (emended from Tsien 1969): Conical corallum having 42 septa of each order at a diameter of 20 mm. Major septa thickened in the outer dissepimentarium, minor septa very short. Dissepimentarium narrow. Tabularium made of variously developed tabulae.

Description: Solitary conical to cylindrical coral often scolecoid (Fig. 4h), up to 38 mm in diameter, with tabularium up to 20 mm in diameter, having up to 45 septa of each order in mature stages (Fig. 5). Major septa short, withdrawn from the axis, straight or curved, thin in the tabularium and slightly thickened in the dissepimentarium (Fig. 6k–l). Minor septa half as long as the major ones, entering into the tabularium. Cardinal and counter major septa not different from the other septa. Cardinal-lateral septa bent towards the cardinal fossula (Fig. 6k). Dissepimentarium made of one or rarely two rows of narrow lonsdaleoid dissepiments and 1–2 rows of concentric interseptal dissepiments usually slightly thickened (Fig. 6j). In longitudinal section, lonsdaleoid dissepiments elongated (up to 10 mm long, 1 mm high) and other dissepiments short and irregular, all strongly inclined towards the tabularium, forming sub-vertical rows in some specimens (Fig. 6m). Tabularium made of complete, regular, flat or mesa-shaped tabulae (Fig. 6m). Wall 1.2 mm thick where preserved (Fig. 6p).

Discussion: From the same beds, Tsien (1969) erected two *Tabulophyllum* species based on limited material displaying very similar characteristics. The only notable difference reported by the author is a limited thickening of septa in *T. tabulatum* Tsien, 1969 compared to *T. firmatum* Tsien, 1969. Such variation typically varies during ontogeny and it appears that *T. tabulatum* is simply a different growth stage of *T. firmatum*.

Tabulophyllum tabulatum differs from *T. lissingenensis* (Birenheide, 1974) that coexists in the same beds by its smaller size, and its narrower dissepimentarium. It also differs from the juvenile stages of the latter by a lower number of septa at the same diameter. *T. bonarense* Schröder and Soto, 2003 from the upper Emsian La Vid Group of the Cantabrian Mountains, differs by its smaller size (< 20 mm) its septa withdrawn from the axis and its narrower dissepimentarium. *T. manifestum* (Spasskiy, 1970) from the lower Eifelian of the Ural Mountains is smaller and simpler as well, with a poorly developed lonsdaleoid dissepimentarium. *T. irregulare* (Różkowska, 1954), from the upper Emsian to lowermost Eifelian of Poland differs in having fewer septa for a similar diameter (40 major septa at 28 mm) but, like *T. tabulatum*, has long minor septa and few lonsdaleoid dissepiments.

Distribution: *Tabulophyllum tabulatum* is only reported from the upper part of the Eau Noire Member, and the upper part of the Emsian *patulus* Zone) in the Ardennes. Soto (1984) indicates *Papiliophyllum* aff. *tabulatum* (Tsien, 1969) in a faunal list for the Eifelian part of the Moniello Formation of the Cantabrian Mountains but without illustration, making the determination uncertain.

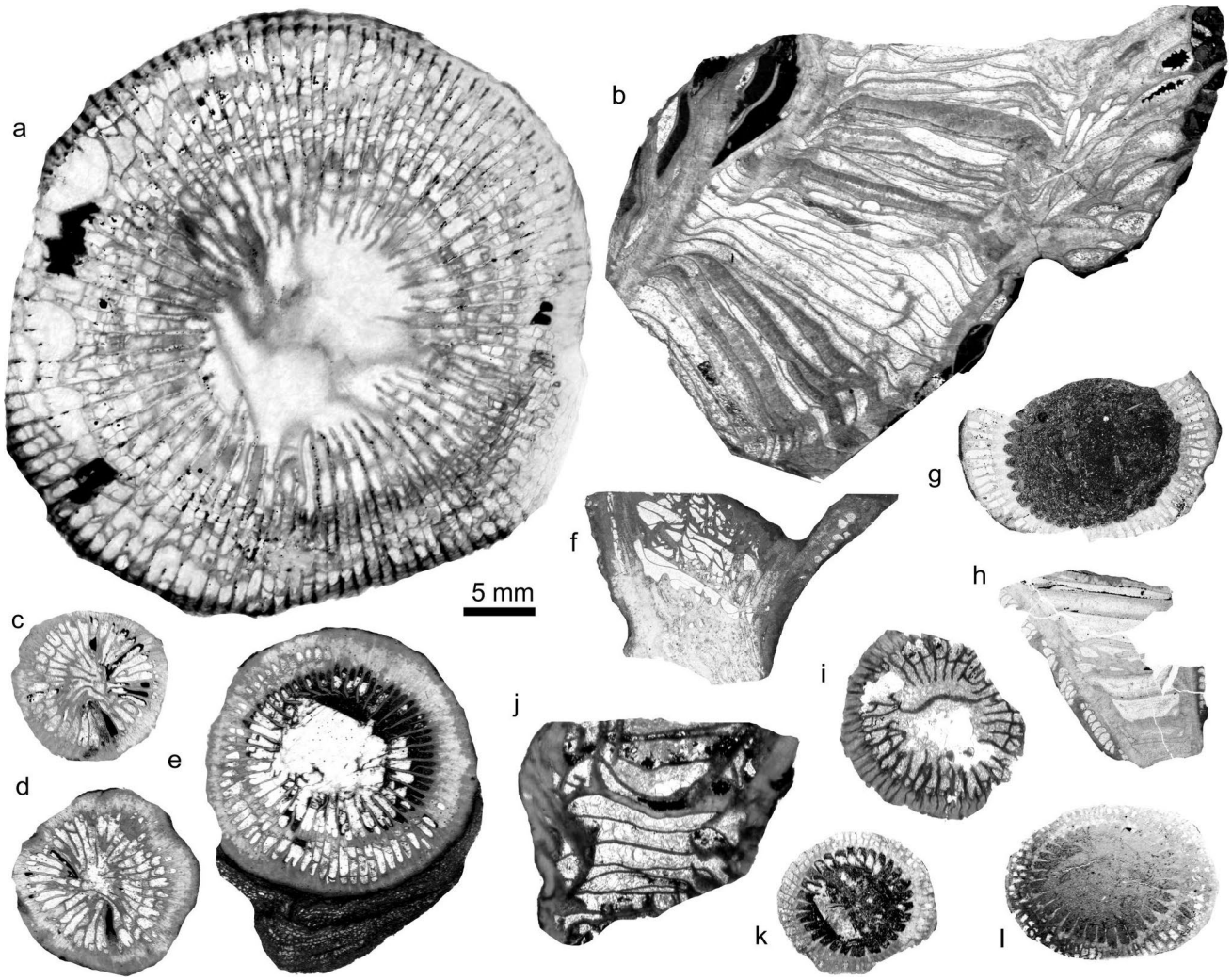


Fig. 7 **a–b** *Tabulophyllum lissingenensis* (Birenheide, 1974), from the Eau Noire Member, Halma section. **a** Specimen WZH/1 in transverse section (TS). **b** Specimen WZH/25 in longitudinal section (LS). **c–e** Cf. *Chostophyllum* sp., CEN-A/2, from the Eau Noire Member, Eau Noire River section, successive TS. **f** Holotype of *Breviphyllum dilatatum* Tsien, 1969, specimen 3221 (IRSNB, coll. Tsien) from the Eau Noire Member, Eau Noire River section, LS. **g–h** Holotype of *Breviphyllum planitabulatum* Tsien, 1969, specimen 3221 (IRSNB, coll. Tsien), g in TS, h in LS. **i–j** *Breviphyllum planitabulatum*, WZH/4-II, i in TS, j in LS. **k–l** *Kunthia crateriformis* Schlüter, 1885, from the Eau Noire Member. **k** Specimen OTB/3, Olloy section, TS. **l** Specimen CRB/1, Couvin section, TS

Breviphyllum Stumm, 1949

Type-species: *Amplexus lonensis* Stumm, 1937 from the uppermost Pragian to the lowermost Emsian of Nevada.
Diagnosis: See Pedder (2002).
Remark: Pedder (1982) considered that Tsien (1969) misinterpreted *Breviphyllum* in including corals with dissepiments. However, in his revision of the genus, Pedder (2002) restricted *Breviphyllum* to corals with elongated dissepiments although this character is not stable as illustrated by Pedder (2002, pl. 1, fig. 2). The Belgian material might not be congeneric with the North American one. In both cases, they are rather rare corals, known only through a limited number of specimens and in need of more detailed investigation.

Breviphyllum planitabulatum Tsien, 1969
(Fig. 7f–j)

* 1969 *Breviphyllum planitabulatum*; Tsien, p. 49, pl. 8, figs 4, 7–8, pl. 20, figs 3–8
1969 *Breviphyllum dilatatum*; Tsien, p. 50, pl. 49, fig. 6

Holotype: Specimen 3221 figured in Tsien (1969, pl. 49, figs 3–8).

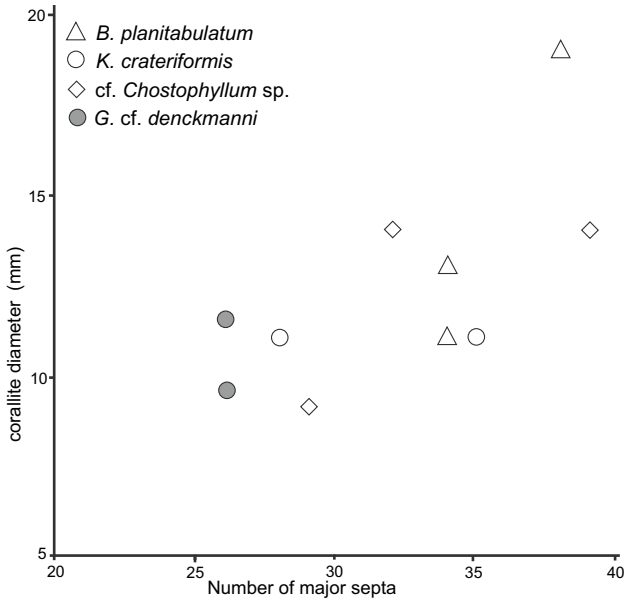


Fig. 8 Corallite diameter plotted against the number of major septa for the species *Breviphyllum planitabulatum, Kunthia crateriformis*, cf. *Chostophyllum* sp. and *Grypophyllum* cf. *denckmanni*

Type locality and horizon: Section on the left bank of the Eau Noire River in Couvin, upper part of the upper Emsian Eau Noire Member ('Co1c') (Tsien 1969).
Remark: Tsien (1969) established two species based on two specimens from the Eau Noire Member: *Breviphyllum planitabulatum* (with relatively spaced horizontal tabulae) and *B. dilatatum* (with thickened septa). Both characters are purely ecological and should not be used for taxonomy. Although the species is uncommon, recently collected material shows that Tsien's specimens represent the same, variable species, both have relatively flat tabulae, and therefore, are conspecific. The type specimen of *B. dilatatum* is only known from a longitudinal section, the transverse one being lost. Therefore, we here propose to consider *B. planitabulatum* as valid, with both longitudinal and transverse sections (though the latter is cut in the calice) preserved from the type specimen (Figs 7g–h).
Material: A single corallum from the Eau Noire Member (Eau Noire River section) in addition to the type specimen.
Diagnosis (emended from Tsien 1969): Solitary coral with wide tabularium, having septa strongly thickened in the dissepimentarium, forming a thick stereozone.
Description: Small ceratoid corallite with deep calice, 19 mm in diameter, having a maximum of 38 septa of each order (Fig. 8). In juvenile stages, septa dilated near the wall (Fig. 7i), bent towards the fossula in cardinal quadrants and radially disposed in counter quadrants. In mature stages, major septa withdrawn from the axis (Fig. 7g). Dissepimentarium made of a single row of small thickened concentric interseptal dissepiments. Wall smooth, thick. In longitudinal section, dissepiments bulbous, almost horseshoe-like, disposed in sub-vertical row (Fig. 7h). Tabularium made of flat horizontal tabulae.
Discussion: *Breviphyllum planitabulatum* Tsien, 1969 is similar to *B. asiaticum* Alkhovik and Ivanowsky, 1988 from the Pragian of Yakutia but the latter is smaller (only 13 mm for the Russian species) and has thicker septa. Both "*Campophyllum*" *lindstroemi* (Frech, 1886) in Hill (1942b) and *B. mirourum* Blake, 2010 from the Middle Devonian of Eastern Australia are larger (24-30 mm) and lack the septal thickening near the wall and on the dissepiments.
Distribution: The species is only known from the upper part of the Eau Noire Member.

Family Disphyllidae Hill, 1939
Kunthia Schlüter, 1885

Type-species: *Kunthia crateriformis* Schlüter, 1885 from the Middle Devonian of the Eifel Hills.
Remark: Wang (1950), Birenheide (1978) and Pedder (1982) regarded *Kunthia* Schlüter, 1885 as synonymous with *Temnophyllum* Walther, 1928 but Pickett (1967) and Schröder (1997) restudied Schlüter's type material and concluded that *Kunthia* differs from *Temnophyllum* in its typically deep calice and the development of carinae (see Schröder 1997 for complete discussion).

Kunthia crateriformis Schlüter, 1885
(Figs 4l, 7k–l)

* 1885 *Kunthia crateriformis*; Schlüter, p. 7–8
1969 *Kunthia crateriformis* Schlüter, 1885; Tsien, p. 47, pl. 8, figs 12–13, pl. 51, fig. 21
non 1969 *Kunthia crateriformis* Schlüter, 1885; Tsien, p. 47, pl. 50, fig. 2, pl. 52, fig. 9
1997 *Kunthia crateriformis* Schlüter, 1885; Schröder, p. 11, pl. 2, fig. 15–19 [*cum. syn.*]

Lectotype: Specimen GPIBO, unsectioned specimen, figured in Schröder (1997), pl. 2, fig. 19a–b.
Type-locality and horizon: Dolendorf Syncline, probably Eifelian Freilingen Formation (Schröder 1997).
Material: Three coralla from the top of Eau Noire Member (one from Olloy and two from the Eau Noire River section).
Diagnosis: See Schröder (1997).
Description: Small turbinate coral with deep calice (Fig. 4l). Mature stage below the calice < 11 mm in diameter with 30–35 septa of each order and tabularium 9 mm wide (Fig. 8). Major septa short, thickened, with sharp ends, slightly carinate in the dissepimentarium. Minor septa poorly to not developed, interrupted by second-order lonsdaleoid dissepiments. Dissepimentarium narrow, made of two rows of concentric dissepiments, the inner row being

strongly thickened (Figs 7k–l). Wall up to 0.8 mm thick. Tabularium only developed in apex, not observed in the thin section here.
Discussion: This material is very similar to the specimens figured by Tsien (1969) as *Kunthia crateriformis* Schlüter, 1885. Schröder (1997) considered that Tsien's specimens lack carinae but the development of the latter is very variable, even in the topotypes (e.g. Schröder's plate 2, figure 16 having small carinae only in one quadrant).
Distribution: Uppermost Emsian-lowermost Eifelian in the Ardennes, Eifelian of the Eifel Hills (Freilingen Formation, Schröder 1997).

Family Charactophyllidae Pedder, 1972
Chostophyllum Pedder, 1982

Type-species: *Chostophyllum metula* Pedder, 1982 from the upper Eifelian and lower Givetian of Western Canada.
Diagnosis: See Pedder (1982).

Cf. *Chostophyllum* sp.
(Figs 7c–e)

Material: Three coralla from the Eau Noire Member (one specimen from Dion, one from Halma and one from Jemelle).
Description: Small cerato-cylindrical solitary coral up to 14 mm in diameter with tabularium 9 mm in diameter, having 30–35 septa of each order (Fig. 8). Major septa thick, fused in the axial area, withdrawn in later stages of growth (Figs 7c-e). Minor septa long, thickened. In mature stages, all septa spindle-shaped and non-carinate. Cardinal major septum shorter and thicker than other septa. Cardinal lateral septa bent towards cardinal fossula. Dissepimentarium made of 1–3 rows of concentric interseptal dissepiments, the inner row being thickened in continuity with the septa (Fig. 7e). Tabulae relatively complete and flat where the septa are withdrawn (Fig. 7j).
Discussion: The mature stages display withdrawn septa and regular dissepiments, hence they are very similar to those observed in species of the genus *Chostophyllum* Pedder, 1982, but in which the juvenile stages differ in having long septa fused in the axis. In that character, the material is similar to *Huanophrentis* Sun, 1958 but the latter is typically undissepimented. The present specimens are therefore attributed to *Chostophyllum* with caution, knowing additionally that this genus is typically found in the lowermost Givetian strata (Pedder 1982).

Family Stringophyllidae Hill, 1939
Genus *Stringophyllum* Wedekind, 1922

Type species: *Stringophyllum normale* Wedekind, 1922, from the Givetian of Sauerland, Germany.
Diagnosis: see Coen-Aubert (2011).

Stringophyllum inflatum Tsien, 1969
(Figs 4i, 9f–k)

*1969 *Stringophyllum inflatum*; Tsien, p. 36, pl. 2, fig. 6, pl. 3, fig. 1, pl. 48, figs 5–6
1969 *Stringophyllum isactis* (Frech, 1886); Tsien, p. 31, pl. 1, figs 2–3, p. 2, fig. 4
1974 *Stringophyllum inflatum*; Tsien, p. 266, fig. 11
1974 *Stringophyllum multiseptatum*; Tsien, p. 268, fig. 12

Holotype: Specimen 9235 figured in Tsien (1969), pl. 3, fig. 1 and Tsien (1974), fig. 11.
Type locality and horizon: Outcrop 700 m south of Petigny village near Couvin, upper part of the upper Emsian Eau Noire Member ('Co1c') (Tsien 1969).
Material: Twelve coralla from the top of the Eau Noire Member (nine specimens from the Halma section, two from Waha and one from the Eau Noire River section) and three corallites from the base of the Villers-la-Tour Member (Villers-la-Tour section). The type specimen of *S. inflatum*, from the Eau Noire Member, is also included.
Diagnosis (emended from Tsien 1974): Solitary but commonly gregarious cylindrical coral, 20 mm in diameter, having up to 45 major septa, long and strongly dilated in dissepimentarium. Minor septa poorly developed. Tabulae complete or incomplete, concave.
Description: Solitary cylindrical coral 15–20 mm in diameter (Fig. 4i), having 35–45 septa of each order (Fig. 10). Major septa straight or curved, reaching the axis and fading axially into isolated trabeculae (Figs 9a, c, e), thickened in the dissepimentarium and commonly also in the tabularium. Cardinal major septum similar to or shorter than the other septa. Minor septa variously developed, usually only present in cardinal quadrants or appearing as septal crests on the wall and dissepiments (Fig. 9b). Cardinal fossula rarely conspicuous. Dissepimentarium narrow, made of a single row of concentric interseptal dissepiments, thickened up to the wall in some specimens. Wall up to 1 mm thick. In longitudinal section, dissepiments 2 mm long and 0.8 mm high, forming a single sub-vertical row (Fig. 9d). Tabularium made of subcomplete concave tabulae, regularly spaced (12-15 tabulae per vertical centimetre) (Fig. 9d).
Discussion: This small *Stringophyllum* with a narrow dissepimentarium looks like isolated branches of *Sociophyllum isactis* (Frech, 1886) and was identified as such by Tsien (1969). In the original description, Tsien (1969) indicated that both species occur in weak aggregates, meaning for him small

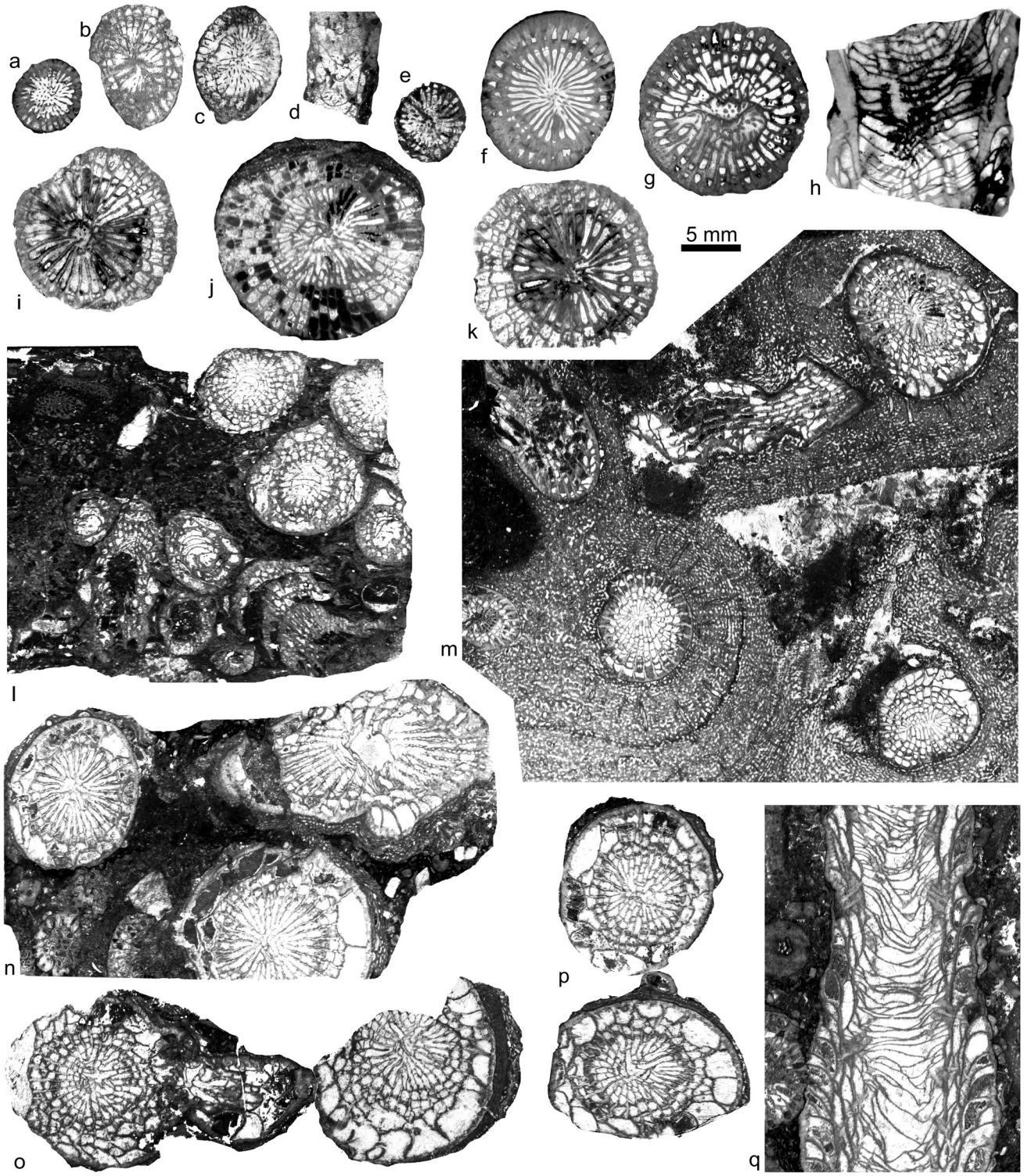


Fig. 9 **a–e** *Stringophyllum crassum* Tsien, 1969 from the Eau Noire Member. **a** Holotype, specimen 24562 (IRSNB, coll. Tsien), Eau Noire River section, in transverse section (TS). **b** Specimen CEN-A/1, Eau Noire River section, TS. **c** Specimen CEN-A/7, Eau Noire River section, TS. **d** Specimen WZH/26, Halma section, in longitudinal section (LS). **e** Specimen WZH/25, Halma section, TS. **f–k** *Stringophyllum inflatum* Tsien, 1969, from the Eau Noire Member. **F** Holotype, 9235 (IRSNB, coll. Tsien), Eau Noire River section, TS. **g–h** Specimen CEN-A/7, WZH/23, Halma section, g in TS, h in LS. **I** Specimen WZH/4, Halma section, TS. **j** Specimen WZH/24, Halma section, TS. **k** Specimen WZH/5, Halma section, TS. **l** *Sociophyllum rolfwerneri* Birenheide, 1979, specimen WPE-III-F/1 from the Wancennes Formation, Wancennes section, TS. **m–q** *Sociophyllum koenigshofi* sp. nov. from the Villers-la-Tour Member. **m** Specimen CE-I/2, Cul d'Efer section, TS. **n** Specimen VTR-I/3, Villers-la-Tour railway section, TS. **o–p** Specimen VTR-I/16, Villers-la-Tour railway section, TS. **q** Specimen VTR-I/5-II, Villers-la-Tour section, LS

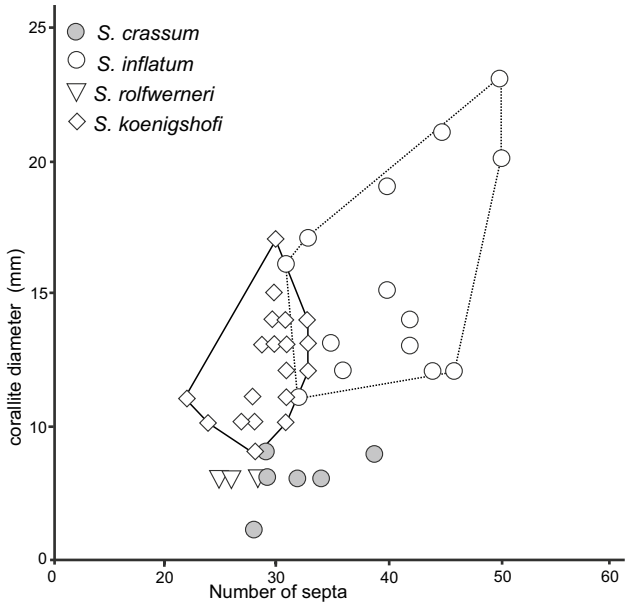


Fig. 10 Corallite diameter plotted against the number of major septa for the species *Stringophyllum crassum, S. inflatum, Sociophyllum rolfwerneri* and *S. koenigshofi*

colonies but no offsets are to be found in the type material or in the collection of specimens studied here. Although, these corals often occur in accumulations, suggesting a gregarious mode of life, there is no evidence that Tsien's material is colonial. Therefore, it is not conspecific with the late Givetian species *S. isactis* as suggested by Coen-Aubert (1999).

Stringophyllum multitabulatum Tsien, 1974, represented by a single specimen collected in exactly in the same horizon as *S. inflatum,* and was considered larger (up to 30 mm in diameter) by Tsien (1974) than typical *S. inflatum.* However, Tsien's collection is very limited and it does not cover the range of variability of the corals. In the present collection, specimens attributed to *S. inflatum* display a continuum of size from c. 10 to 30 mm (Fig. 10). Moreover, the densely-packed tabulae are clearly a character varying with ecological conditions, also shown in a larger collection of specimens. *S. inflatum* differs from *S.* cf. *schwelmense* (Wedekind, 1925) collected from the Eifelian Junckerberg Formation by Schröder (1998) by a slightly larger diameter and minor septa less developed.

Distribution: *Stringophyllum inflatum* has not been reported outside the type area of the Ardennes where the species occurs in the upper part of the Eau Noire Member and lowermost part of the Villers-la-Tour Member, straddling the Emsian-Eifelian boundary.

Stringophyllum crassum Tsien, 1969 *non* Yü and Kuang, 1982
(Figs 4n, 9a–e)

*1969 *Stringophyllum crassum*; Tsien, p. 37, pl. 2, fig. 5, pl. 3, figs 3–4, pl. 48, fig. 3

Holotype: Specimen n° 24562 figured in Tsien (1969), pl.3, fig. 4.

Type locality and horizon: Section on the left bank of the Eau Noire River in Couvin, upper part of the upper Emsian Eau Noire Member ('Co1c') (Tsien 1969).

Material: Seven coralla from the top of the Eau Noire Member (four specimens from the Halma section, one from Olloy and two from the Eau Noire River section), in addition to the type specimen of the species.

Diagnosis (emended from Tsien 1969): Sub-cylindrical solitary coral up to 10 mm in diameter and 20 mm high, having a cup-shaped calice. Major septa long, divided into trabeculae in the tabularium. Minor septa not developed.

Description: Small cylindrical coral less than 10 mm in diameter (Fig. 4n), usually elliptical in transverse section, having 28–32 septa (Fig. 10). Major septa long, reaching the axis where they divide into isolated trabeculae (Figs 9f–g). Cardinal major septum and fossula inconspicuous. Minor septa rarely developed (Fig. 9i). Base of septa thick and cuneiform. Dissepimentarium made of 0–2 rows of small concentric dissepiments in mature stages (Figs 9j–k). Wall up to 0.5 mm thick. In longitudinal section, tabulae complete, concave, and regularly spaced (Fig. 9h).

Discussion: Tsien (1974) stated that *Stringophyllum crassum* Tsien, 1969 is a juvenile corallite of *S. inflatum* Tsien, 1969 that occurs in the same beds. However, juvennle stages of *S. crassum* differ in the absence of minor septa (they are usually developed, at least in some quadrants in *S. inflatum*) and by a more simple dissepimentarium made of interseptal dissepiments only.

The only described species with such small coralla is *Stringophyllum elegantum* Wang, 1948 from the Middle Devonian of Yunnan but the latter is characterised by a long cardinal major septum and minor septa 2/3 as long as the major ones. The present species is conversely characterised by minor septa virtually absent.

Distribution: *Stringophyllum crassum* has not been reported outside the type area of the Ardennes.

Sociophyllum Birenheide, 1962

Type-species: *Spongophyllum elongatum* Schlüter, 1881 from the lower Givetian of the Eifel Hills.

Diagnosis: see Birenheide (1978).

Sociophyllum rolfwerneri Birenheide, 1979
(Fig. 9l)

*1979 *Sociophyllum semiseptatum rolfwerneri*; Birenheide, p. 202, pl. 6, fig. 8, pl. 12, fig. 19

?1989 *Sociophyllum rolfwerneri* Birenheide; Coen-Aubert, p. 26, pl. 4, figs 21–27
2012 *Sociophyllum semiseptatum rolfwerneri* Birenheide; Ernst et al., p. 739, figs 3i, 4a–c

Holotype: Specimen n° SMF 34220 figured in Birenheide (1979), pl. 6, fig. 8.
Type locality and horizon: Outcrop on the northern side of the Honert, in the Blankenheim Syncline, Eifel Hills, Germany, basal Eifelian Lauch Formation (Birenheide, 1979).
Material: One fragment of colony from the basal part of the Wancennes Formation (Wancennes section).
Diagnosis: See Birenheide (1979).
Description: Small dendroid colony with sub-cylindrical corallites, elliptical in transverse section, with a relative conspicuous bilateral symmetry. Mature corallites 8 mm in diameter, tabularium 4–5 mm in diameter, having 25–26 septa (Fig. 10). Major septa long, reaching the axial zone but leaving a narrow elongated free space. Bases of septa thick, with thickness decreasing towards the axis. In some specimens, septa divide axially as isolated trabeculae. Cardinal major septum slightly shorter. Minor septa seldom developed, incomplete or appearing as aligned isolated trabeculae, mostly in cardinal quadrants. Dissepimentarium made of one complete row and often an additional incomplete row of large lonsdaleoid dissepiments and 1–5 rows of concentric interseptal dissepiments, one or two rows being thickened (Fig. 9l). Wall 0.5 mm thick. In longitudinal section, dissepiments variable in size, strongly inclined towards the tabularium. Tabularium more or less complete, concave, densely packed (30 tabulae per vertical centimetre), and tabulae regularly spaced. Increase lateral non-parricidal with offsets having few septa and irregular vesicular dissepiments.
Discussion: This specimen displays a smaller dissepimentarium than *S. rolfwerneri* Birenheide, 1979 but as the available material is limited and it might simply be the effect of a section through a juvenile stage of the colony.
Distribution: The present material is present in the basal part of the Wancennes Formation. Similar, yet undescribed material, has been collected higher in the formation. *S. rolfwerneri* is described from strata of similar age (lower Eifelian) Lauch Formation from the Eifel Hills (Birenheide, 1979, 1962) and Remscheid Formation of Sauerland (Ernst et al. 2012).

Sociophyllum koenigshofi sp. nov.
(Figs 3c, 9m–q)

? 1969 *Stringophyllum acrophylloides* (Borchers *in* Wedekind, 1925); Tsien, p. 32, pl. 4, figs 5a–b.
p.p. 1974 *Stringophyllum elongatum* Schlüter, 1881; Tsien, p. 264, figs 6.3a–b.

Origin of name: This species is dedicated to Peter Königshof, a celebrated researcher of the Devonian palaeontology, stratigraphy, sedimentology and more.
Holotype: Colony VTR I/13-I from Villers-la-Tour, 3 transverse and one longitudinal section.
Type locality and horizon: Section along the disused railway east of Villers-la-Tour, lower Eifelian Villers-la-Tour Member.
Material: In addition to the holotype, fragments of six colonies from the basal part of the Villers-la-Tour Member (Villers-la-Tour section and from the Cul d'Efer section). The material figured by Tsien (1974) is lost and its stratigraphical position is not precisely known.
Diagnosis: Weakly dendroid colonies with sub-cylindrical corallites with bilateral symmetry, 14 mm in alar diameter, having 32 long major septa. Minor septa poorly developed. Dissepimentarium made of lonsdaleoid dissepiments subhorizontal near the wall and plunging towards the tabularium. Tabulae flat or slightly concave.
Description: Small dendroid colonies with few sub-cylindrical corallites with bilateral symmetry. Corallites 13–15 mm in diameter, tabularium 7–8 mm in diameter, having 30–33 septa of each order (Fig. 10). Major septa long, reaching the axial zone, usually divided axially in isolated trabeculae (Fig. 9n). Septa bent towards the cardinal septum in cardinal quadrants and radially disposed in counter quadrants, sinuous to tortuous in the tabularium, interrupted in the periphery by lonsdaleoid dissepiments and splitting into isolated trabeculae in the outer dissepimentarium (Figs 9o–p). Counter major septum long and straight. Cardinal major septum shorter. Minor septa poorly developed, always short. Bases of septa resting on lonsdaleoid dissepiments or appearing as short spines on the wall. Dissepimentarium made of two rows of large irregular lonsdaleoid dissepiments (Fig. 9m), larger in the outer row than in the inner one, and 1–2 rows of small concentric, usually thickened, interseptal dissepiments. Wall straight and smooth, up to 0.8 mm thick. In longitudinal section, outer dissepiments with a marked shoulder, with a sub-horizontal outer side and sub-vertical inner side (Fig. 9q). Inner rows steeply declined towards the tabularium. Tabularium depressed, made of horizontal flat to concave tabellae regularly spaced (20 tabellae per vertical centimetre) and clinotabellae (Fig. 9q). Increase lateral, non-parricidal, with offsets developing lonsdaleoid dissepiments and trabeculae before septal blades (Fig. 9o).
Discussion: The present material is similar to the lower Givetian species *Sociophyllum elongatum* (Schlüter, 1881) with marked bilateral symmetry and comparable size and number of septa but differs in the reduced lonsdaleoid dissepimentarium, less concave tabulae and septa appearing as isolated trabeculae in the outer dissepimentarium. *S. koenigshofi* can be compared to *S. crassum* Yü and Kuang, 1982 but the latter differs by the near absence of minor septa and

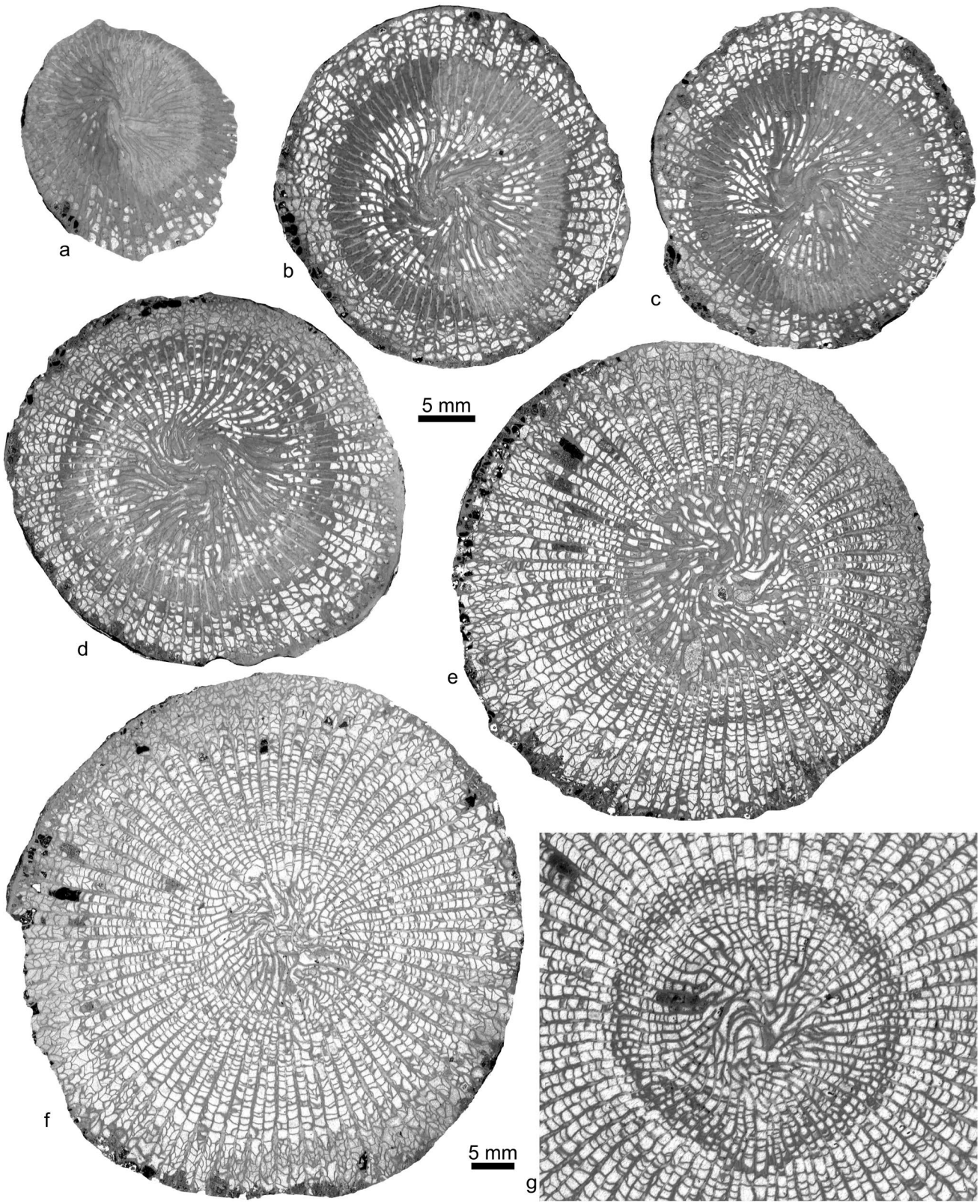


Fig. 11 **a–g** *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851), from the Eau Noire Member, Waha section. **a–f** Specimen W3, successive transverse sections (TS), x2. **g** Close-up view of the axial vortex, same specimen, TS

the strong thickening of skeletal elements. This new species differs from *S. rolfwerneri* which is found in the equivalent horizon in Belgium and Germany in its larger size and its septa more developed (they are shorter and scarcely developed in *S. rolfwerneri*).

Distribution: The species is only known from the type locality and horizon. The specimen figured by Tsien (1969) as *Stringophyllum acrophylloides* (Wedekind, 1925) is possibly conspecific (the thin section is lost and the material only figured as hand drawings) and comes from a slightly younger horizon (Cul d'Efer Member). The specimen attributed by Tsien (1974) to *Stringophyllum elongatum* is from the younger Jemelle Formation.

Family Ptenophyllidae Wedekind, 1923
Genus *Acanthophyllum* Dybowski, 1873

Type species: *Cyathophyllum heterophyllum* Milne-Edwards and Haime, 1851 from the Middle Devonian of the Eifel Hills.

Diagnosis: See Birenheide (1978).

Acanthophyllum heterophyllum (Milne-Edwards and Haime, 1851)
(Figs 4e, m, 11a–g, 12a-b)

*1851 *Cyathophyllum heterophyllum*; Milne-Edwards and Haime, p. 367, pl. 10, figs 1a–b
1999 *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851); Pedder, 1999, p. 403, pl. 9, figs 1–4, 6, 9 [*cum. syn.*]
2011 *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851); Coen-Aubert, p. 36, pl. 2, fig. 6
2017 *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851); Coen-Aubert, p. 267, pl. 1, figs A–B
2020 *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851); Jamart and Denayer, p. 289, fig. 5F
2022 *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851); Coen-Aubert, p. 60, pl. 4, figs C–D

Holotype: Specimen MNHN, LP S 11670 figured by Milne-Edwards and Haime (1851), pl. 10, fig. 1a-b and photographically illustrated by Coen-Aubert (1997), pl. 1, figs 1-2.

Type locality and horizon: Hillesheim Syncline, Eifel Hills, most probably from the Eifelian Junkerberg Formation (Birenheide 1961).

Material: Twenty-two coralla from the top of the Eau Noire Member (nine specimens from Waha, four from Dion, one from Olloy and eight from the Eau Noire River section) and two specimens from the Villers-la-Tour Member (Villers-la-Tour section).

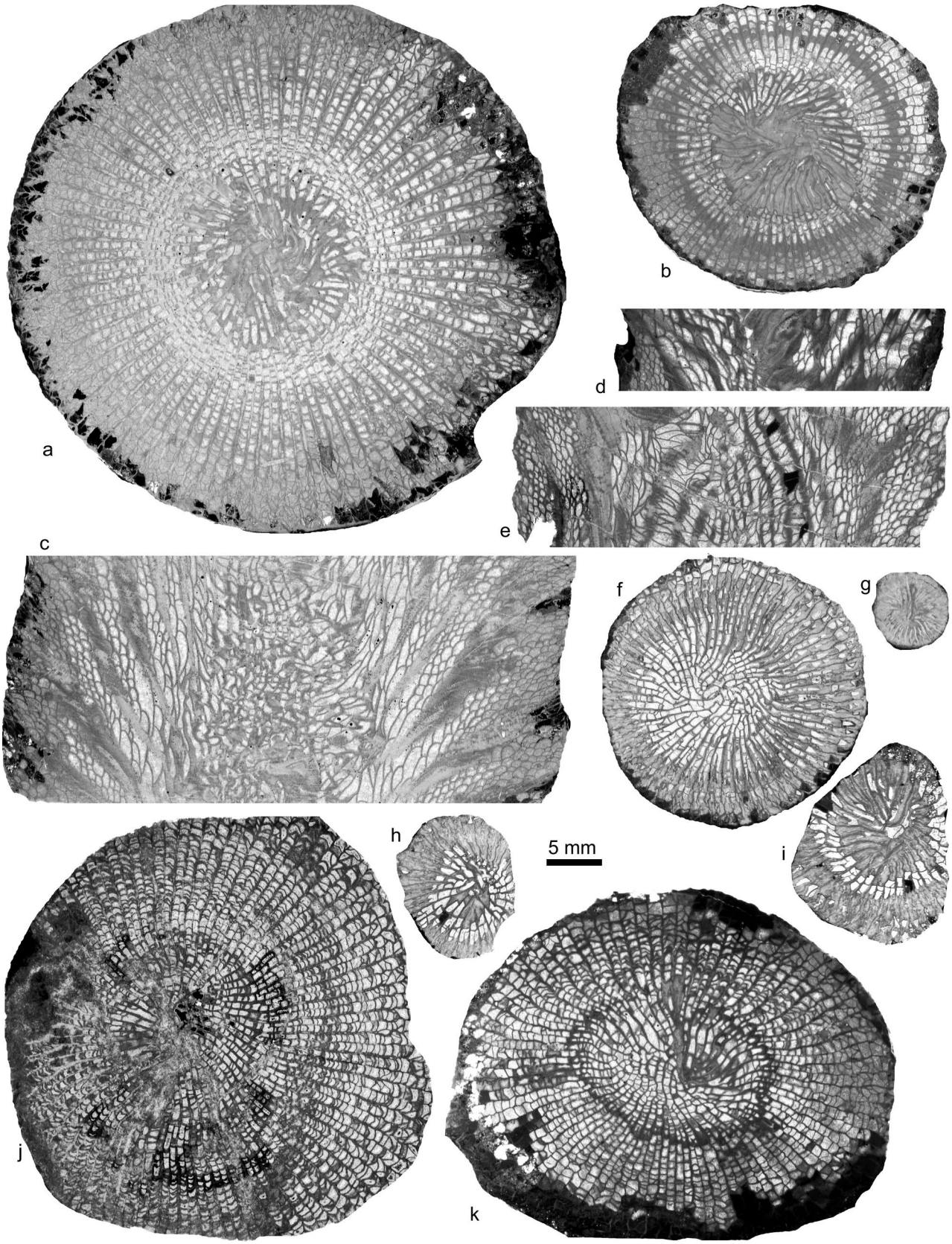
Diagnosis: See Coen-Aubert (1997).

Description: Large trochoid to cylindrical solitary coral (Figs 4e, m), circular or elliptical in transverse section, reaching 50 mm in diameter with tabularium 15-18 mm in diameter, having up to 50 septa of each order in mature stages (Fig. 13). All septa spindle-shaped in dissepimentarium, straight except near the wall where they can be undulose (Figs 11e–f). Major septa very long, twisted in the axial area, some joined and connected by stereoplasmic thickening, forming an axial vortex (Figs 11b–d, f–g). Axial ends irregularly thickened and rhopaloid. Cardinal and counter major septa usually thicker in dissepimentarium with their axial ends spindle-shaped. Minor septa long, entering into tabularium, typically thinner than the major ones (Figs 11e–f, 12a). Cardinal fossula rarely conspicuous, with limited withdrawal of dissepimentarium. Dissepimentarium complex, made of numerous rows of small interseptal dissepiments. Outer 5–10 rows of herringbone and arched dissepiments also include pseudonaotic and dissepiments parallel to septa. Middle part of the dissepimentarium composed of 5–20 rows of concentric and herringbone dissepiments. Innermost rows made of small concentric interseptal dissepiments, thickened in continuity with septa in some corallites. In juvenile stages, stereoplasmic thickening occurs in the tabularium and dissepimentarium but tends to fade away during ontogeny (Fig. 11). Wall 0.3 mm thick, usually eroded, with cuneiform septal bases. In longitudinal section, dissepiments small and globular, 1 mm high and large, sub-horizontal in the outer dissepimentarium, more inclined towards the tabularium with innermost rows subvertical (Fig. 12c). Tabularium strongly concave, made of numerous small vesicular tabellae, strongly divided by the axial part of septa. Peripheral tabellae strongly inclined, and axial ones more horizontal. Clinotabellae occur sporadically.

Discussion: *Acanthophyllum heterophyllum* is the largest species of the genus occurring in the studied beds. Its thick major septa, thin minor septa and axial vortex are distinctive characteristics of the species. *A. vermiculare* is rather similar, though slightly smaller, and has thin septa in the mature stages but has stereoplasmic thickening on the dissepiments near the tabularium margin. *A. radiatum* differs in having thickened septa in the tabularium at all growth stages.

Distribution: *Acanthophyllum heterophyllum* is a species widely distributed in the Eifelian of NW Europe as summarised by Coen-Aubert (2011). Its occurrence in upper Emsian strata is less documented. Besides the Ardennes, it is present in the Emsian of the Carnic Alps (Charlesworth 1914) and the Ural Mountains (Spasskiy 1977).

Acanthophyllum vermiculare (Goldfuss, 1826)
(Figs 4a, d, 12f–g, j–k)


a
b
c
d
e
f
g
h
i
j
k
5 mm

◂**Fig. 12** **a–d** *Acanthophyllum heterophyllum* (Milne-Edwards and Haime, 1851) from the Eau Noire Member. **a–b** Specimen W/18, Waha section, a in transverse section (TS), b in longitudinal section (LS). **c–d** Specimen OTB/13, Olloy section, successive TS. **e, h–i** *Acanthophyllum radiatum* (Wedekind, 1924) from the Eau Noire Member. **e** Specimen W/5, Waha section, TS. **h–i** Specimen SN-II/4, Sohier section, successive TS. **f–g, j–k** *Acanthophyllum vermiculare* (Goldfuss, 1826) from the Eau Noire Member. **f** Specimen W/9, Waha section, LS. **g, j** Specimen Di-III/13, Dion section, **g** in LS, j in TS. **k** Specimen W/9, Waha section, TS

* 1826 *Cyathophyllum vermiculare*; Goldfuss, p. 58, pl.17, fig. 4

1889 *Cyathophyllum torquatum* Schlüter, 1884; Schlüter, p. 293, pl. 4, figs 1–3

non 1934 *Cyathophyllum torquatum* Schlüter, 1884; Le Maître, p. 154, pl. 5, figs 16–17

1942 *Ptenophyllum torquatum* (Frech) non Schlüter; Prantl, 1942, p. 2, pl. 1, fig. 1

non 1947 *Acanthophyllum torquatum* var. *orientalis* Reed, 1922 ; Le Maître, 1947, p. 42, pl. 4, figs 2–6

1954 *Ptenophyllum torquatum* (Schlüter, 1889); Różkowska, p. 226, figs 18–22

1961 *Acanthophyllum* (*Acanthophyllum*) *torquatum* (Schlüter, 1884); Birenheide, p. 99, pl. 4, fig. 14

1969 *Acanthophyllum gerosteinense* (Wedekind, 1924); Tsien, p. 113, pl. 43, figs 6–8, pl. 52, fig. 16

p.p. 1969 *Acanthophyllum involutum* (Wedekind, 1924); Tsien, p. 114, pl. 26, figs 1–2

p.p. 1969 *Acanthophyllum vermiculare* (Goldfuss, 1826); Tsien, p. 116, pl. 44, figs 1–5

non 1970 *Acanthophyllum torquatum* Schlüter, 1884; Brice, 1970, p. 292, pl. 18, fig 2

2011 *Acanthophyllum vermiculare* (Goldfuss, 1826); Coen-Aubert, p. 37, pl. 2, figs 1–5, pl. 3, fig. 9 [*cum. syn.*]

2017 *Acanthophyllum concavum* (Walther, 1928); Nose et al., pl. 3, fig. 3

2020 *Acanthophyllum vermiculare* (Goldfuss, 1826); Jamart and Denayer, figs 5A–C

2022 *Acanthophyllum vermiculare* (Goldfuss, 1826); Coen-Aubert, 2022, p. 60, pl. 2, fig. C, pl. 3, figs C–I

Holotype: Specimen GMBo 198 from the Goldfuss collection, figured by Coen-Aubert (1998, pl. 2, fig. 1).

Type locality and horizon: Goldfuss' specimen is probably from Nohn, Hillesheim Syncline, Eifel Hills, lowermost Givetian Ahbach Formation (Coen-Aubert 1998).

Material: Four coralla from the top of the Eau Noire Member (two specimens from Dion, one from Waha and one from the Eau Noire River section).

Diagnosis: See Coen-Aubert (2017).

Description: Middle-sized sub-cylindrical solitary coral (Fig. 4d), often scolecoid (Fig. 4a), sub-elliptical in transverse section, 38–40 mm in diameter, tabularium 16–18 mm in diameter, having 44–48 septa of each order in mature stages (Fig. 13). Major septa very long but varying in length, reaching the axis and twisted (Fig. 12k), thin to slightly thickened. One septum is usually longer (counter septum?). Minor septa long, slightly entering into the tabularium, thinner and straighter than the major ones. Bases of septa embedded in the wall. Dissepimentarium complex, made of numerous concentric, herringbone and arched dissepiments, the innermost row being thickened in some specimens (Fig. 12f). Wall 0.2-0.3 mm thick, often eroded. In longitudinal section, dissepiments of the outer rows globular, < 1 mm long and high, more elongated in the inner rows. Tabularium strongly divided, made of small vesicular tabellae declined in periphery and more horizontal in the axial part, irregularly spaced (10 tabellae per vertical centimetre).

Discussion: Coen-Aubert (1997) and Schröder and Kazmierczak (1999) considered *A. torquatum* (Schlüter, 1884) to be conspecific with *A. vermiculare* (Goldfuss, 1826), as are the species *A. gerolsteinense crassum* (Wedekind, 1924), *A. intortum* (Wedekind, 1923) and *A. praematurum* (Wedekind, 1923). Birenheide (1961, 1962, 1972) considered however, the two species as valid as *A. torquatum* is typically found in the upper Emsian and lower Eifelian strata whereas *A. vermiculare* is typically an upper Eifelian-lower Givetian species. The latter are slightly smaller and thinner than the Emsian material but it is compatible with intraspecific variation. Further comparison of Emsian and Givetian species might be interesting to confirm this statement.

Distribution: *A. vermiculare* is frequent in the upper Eifelian and lower Givetian of Eifel Hills, the Ardennes and

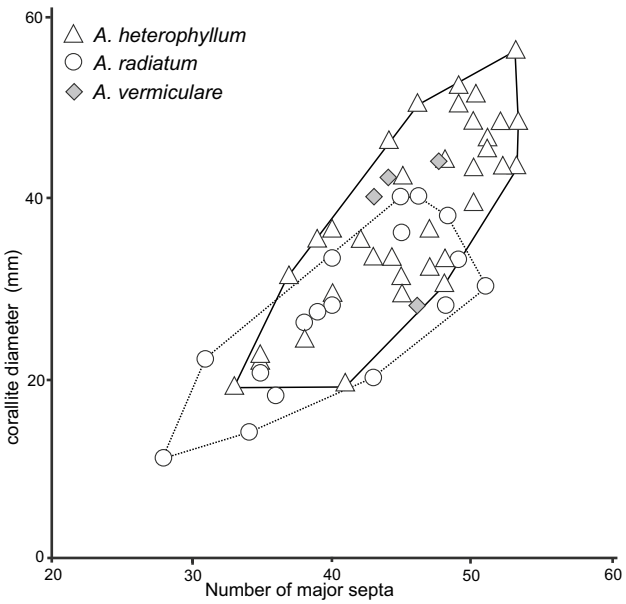
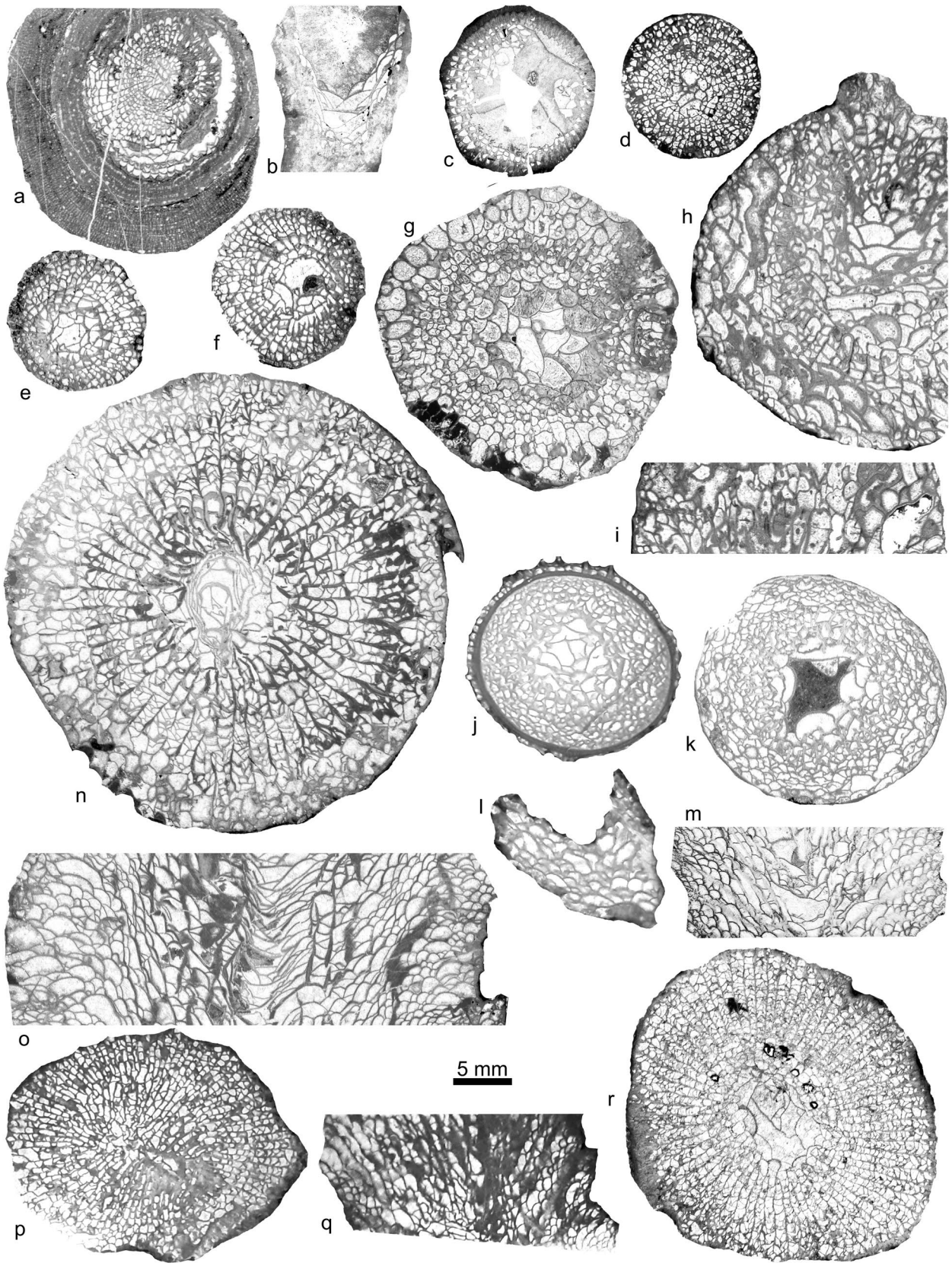


Fig. 13 Corallite diameter plotted against the number of major septa for the species *Acanthophyllum heterophyllum, A. radiatum and A. vermiculare*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5 mm

◂**Fig. 14** **a** *Grypophyllum* cf. *denckmanni* Wedekind, 1922, from the Villers-la-Tour Member, specimen VTR-I/1, Villers-la-Tour railway section, transverse section (TS). **b–f** *Digonophyllum perseptatum* (Tsien, 1969) from the Eau Noire Member. **b-c** Holotype of *Hemicystiphyllum perseptatum* Tsien, 1969, specimen 3212 (IRSNB, coll. Tsien), Eau Noire River section, b in LS, c in TS. d Specimen WZH-II/26-II, Halma section, TS. **e–f** Specimen OTB/12, Olloy section, successive TS. **g–i** *Lekanophyllum punctatum* Wedekind, 1924. **g** Holotype of *Lekanophyllum punctatum* Wedekind, 1924, from the Junkenberg Formation, Auburg, Eifel Hills, thin section WDKD 2716 (Senckenberg Forschungsinstitut, coll. Wedekind), in TS. **h–i** *Lekanophyllum puctatum* Wedekind, 1924, from the Petigny Member, CE-III/6, Petigny rue Augile section, h in TS, i in longitudinal section (LS). **j–m** *Lekanophyllum cylindricum* (Schlüter, 1882), from the Villers-la-Tour Member. **j–k** Specimen VTR-I/25, Villers-la-Tour railway section, j in TS, k in LS. **l** Specimen VTR-I/7, Villers-la-Tour railway section, TS. m Specimen VTR-I/5-II, Villers-la-Tour railway section, LS. **n–o** *Mesophyllum* sp. from the Eau Noire Member, W/17, Waha section, m in TS, n in LS. **p–r** *Digonophyllum* cf. *intermedium* (Vollbrecht, 1926), from the Eau Noire and Villers-la-Tour Members. **p–q** Specimen CEF/1, Eau Noire River section, p in TS, q in LS. **r** Specimen OTB/4, Olloy section, TS

possibly North Africa. Its occurrence in the upper Emsian-lower Eifelian is seemingly restricted to the Ardennes and Eifel Hills (Birenheide 1978).

Acanthophyllum radiatum (Wedekind, 1924)
(Figs 4f, 12e, h–i)

* 1924 *Ptenophyllum radiatum*; Wedekind, p. 41, fig. 58
? 1947 *Acanthophyllum torquatum* var. *orientalis* Reed, 1922 ; Le Maître, p. 42, pl. 4, figs 2–6
1961 *Acanthophyllum (Acantophyllum) radiatum* (Wedekind, 1924); Birenheide,p. 104, pl. 1, fig 1, pl. 5, figs 15–16
p.p. 1969 *Acanthophyllum involutum* (Wedekind, 1924); Tsien, p. 114, pl. 26, fig. 3, pl. 27, fig. 4
1969 *Acanthophyllum radiatum* (Wedekind, 1924); Tsien, p. 115, Pl 45, fig 7, pl. 47, fig 1
1978 *Acanthophyllum radiatum* (Wedekind, 1924); Birenheide, p. 115, pl. 45, fig 7, pl. 47, fig 1

Lectotype: Specimen SMF WDKD.406413, selected by Birenheide (1961), figured by Wedekind (1924), fig. 58.
Type locality and horizon: Nohn-Dankrath road in Dollendorf, Hillesheim Syncline, Eifel Hills, from the Eifelian Nohn Formation (Birenheide 1961).
Material: Ten coralla from the top of the Eau Noire Member (two specimens from Halma, three from Waha, one from Dion, one from Olloy, one from Sohier and two from the Eau Noire River section) and one specimen from the Saint-Joseph Member (Treignes section).
Diagnosis: See Bireheide (1978).
Description: Middle-sized sub-cylindrical (Fig. 4f), often scolecoid, solitary coral commonly elliptical in transverse section, 20–30 mm in diameter, tabularium 11–18 mm in diameter, having 40–50 septa of each order in mature stages (Fig. 13). Major septa long, reaching the axis, spindle-shaped in the dissepimentarium, thinner in the tabularium, twisted and rhopaloid at the axis. Septa thickened both in the dissepimentarium and at its inner margin in some specimens (Figs 12h–i). Counter major septum thicker. Minor septa long, thinner and more sinuous than the major ones. Thickening tends to decrease in mature stages. Dissepimenatrium wide, made of 2–6 outer rows of small herringbone and arched dissepiments and 1–2 rows of concentric interseptal dissepiments, some rows being thickened. Lonsdaleoid dissepiments rare. Wall 0.2–0.3 mm thick, usually eroded. In longitudinal section, dissepiments small, globose in outer rows, more elongated and inclined in inner rows (Fig. 12e). Tabularium incomplete, made of small vesicular, concave tabellae, divided by the septa, regularly spaced (10–12 tabellae per vertical centimetre).
Discussions: *Acanthophyllum radiatum* (Wedekind, 1924) differs from *A. heterophyllum* (Milne-Edwards and Haime, 1851) by its smaller size and similar thickness of the major and minor septa, but more importantly, by the thickening of the septa in the tabularium at sub-mature growth stages. *A. vermiculare* (Goldfuss, 1826), which has a similar size is also distinguished by the lack of septal thickening except in early growth stages. Such a character is usually considered to be ecological, but in this case, it conveniently distinguishes the two species.
Distribution: Besides the Ardennes, the species is known in the upper Emsian to lower Eifelian (Lauch to Nohn Formation) of the Eifel Hills (Birenheide, 1961) where it occurs with *A. vermiculare*. In Belgium, it occurs at a similar stratigraphic level but one specimen, collected from the Saint-Joseph Member is older (lower part of *patulus* Zone).

Grypophyllum Wedekind, 1922

Type species: *Grypophyllum denckmanni* Wedekind, 1922, from the Givetian of Bergish-Gladbach, Germany.
Diagnosis: See Coen-Aubert (2000).

Grypophyllum cf. *denckmanni* Wedekind, 1922
(Fig. 14a)

1969 *Grypophyllym denckmanni* Wedekind, 1922; Tsien, p. 121, pl. 46, figs 7a–b

Material: One corallum from the Villers-la-Tour Member (Villers-la-Tour section).
Description: Cylindrical solitary coral, 10 mm in diameter with 26 septa of both orders (Fig. 8). Major septa are long, thin, and straight, some reaching the axis and connecting, spindle-shaped in dissepimentarium (Fig. 14a). Minor septa long, entering slightly into tabularium.

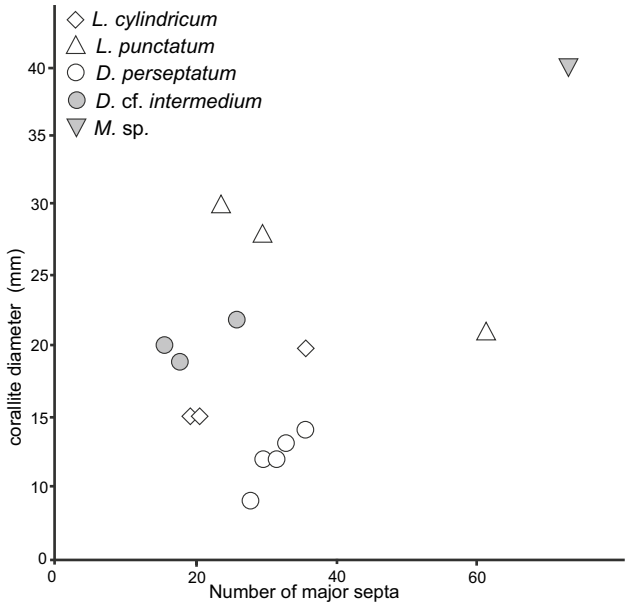


Fig. 15 Corallite diameter plotted against the number of major septa for the species *Lekanophyllum cylindricum, Digonophyllum perseptatum, Digonophyllum* cf. *intermedium, Mesophyllum* sp. and *Zonophyllum duplicatum*

Dissepimentarium made of 8–15 rows of herringbone and concentric dissepiments with occasional irregular lonsdaleoid dissepiments. Wall thick, with cuneiform septal bases.

Discussion: This specimen is slightly smaller than typical *Grypophyllum denckmanni* Wedekind, 1922 with a similar number of septa and displays lonsdaleoid dissepiments. This occurrence of lonsdaleoid dissepiments was pointed out by Coen-Aubert (2000) in several *Grypophyllum* species but not in typical *G. denckmanni*. The present specimen is overgrown by a stromatoporoid and displays rejuvenescences, so the development of lonsdaleoid dissepiments could also be purely ecological. Nevertheless, an intraspecific variation cannot be ruled out. Among the specimens attributed by Tsien (1969) to *G. denckmanni*, only the one figured in his plate 46, figure 7a–b is conspecific with the present material but was excluded from *G. denckmanni* by Coen-Aubert (2000), based on the development of large irregular dissepiments.

Distribution: *G. denckmanni* is typically found in the Givetian strata (see revision by Coen-Aubert, 2000), but occurrences in the Eifelian of the Bohemian Massif have been reported by Galle (1994). The present material as well as part of Tsien's (1969) material comes from the lower Eifelian Villers-la-Tour Member and is probably the oldest reported *Grypophyllum* species.

Family Cystiphyllidae Milne-Edwards and Haime, 1850
Subfamily Digonophyllinae Wedekind, 1923

Lekanophyllum Wedekind, 1924

Type-species: *Lekanophyllum puctatum* Wedekind, 1924, from the upper Eifelian of the Eifel Hills.
Diagnosis: See McLean (2021).

Lekanophyllum cylindricum (Schlüter, 1882)
(Figs 14j–m)

* 1882 *Actinocystis cylindrical*; Schlüter, p. 206
1889 *Mesophyllum cylindricum* (Schlüter, 1882); Schlüter, p. 73, pl. 9, figs 3–4
1964 *Plasmophyllum (Mesophyllum) cylindricum* (Schlüter, 1882); Birenheide, p. 48, pl. 5, figs 17–20, pl. 10, fig. 52, pl. 14, fig. 62, pl. 28, fig. 138 [*cum. syn.*]
1969 *Mesophyllum cylindricum* (Schlüter, 1882); Tsien, p. 99, pl. 38, figs 1–2
? 1969 *Zonodigonophyllum tenuis* (Vollbrecht); Tsien, p. 105, pl. 39, fig. 1
1969 *Paracystiphylloides inconditum*; Tsien, p. 108, pl. 38, fig. 2
? 1975 *Plasmophyllum (Mesophyllum) cylindricum* (Schlüter, 1882); Latipov, 1975, p. 26, pl. 4, fig. 2
1978 *Mesophyllum (Mesophyllum) cylindricum* (Schüter, 1882); Birenheide, p. 163, fig. 101
1997 *Mesophyllum (Mesophyllum) cylindricum* (Schlüter, 1882); Schröder, p. 217, pl. 3, figs 16–17
1998 *Mesophyllum (Mesophyllum) cylindricum* (Schlüter, 1882); Schröder, p. 64, pl. 17, fig. 103

Lectotype: Specimen 184 figured by Schlüter (1889, pl. 7, figs 3–4).
Type locality and horizon: Left bank of the Kyll River at Lissingen, Gerolstein Syncline, Eifel Hills, Eifelian Lauch or Nohn Formation (Schröder 1998).
Material: Two coralla from the basal part of the Villers-la-Tour Member (Villers-la-Tour section).
Diagnosis: See Birenheide (1978).
Description: Conico-cylindrical solitary cystimorph coral, circular in transverse section, 15–20 mm in diameter with a poorly-defined tabularium 8–15 mm in diameter (Fig. 15). Septa variously developed as spines in inner dissepimentarium (Figs 14i–j), 40–50 septal spines in total, not differentiated into major and minor series, short, sinuous, variable in length, interrupted by lonsdaleoid dissepiments. Dissepimentarium made of numerous rows of small and densely-packed lonsdaleoid dissepiments, concentric interseptal dissepiments in inner dissepimentarium. Wall 0.5 mm thick, straight and smooth. In longitudinal section, dissepiments bulbous, irregular, passing to vesicular tabellae forming a concave tabularium (Figs 14k–l).
Discussion: *Lekanophyllum cylindricum* (Schlüter, 1882) is characterised by the development of irregular septa spines,

fused or not into septa, small dissepiments, bulbous tabulae and a relatively small size (12–35 mm). All characteristics can be observed in the present material. The septal spines are one of the most obvious characteristics allowing us to distinguish *L. cylindricum* from small-sized *Nardophyllum* species present in the same beds.

Distribution: *Lekanophyllum cylindricum* is a rather frequent component of the Emsian-Eifelian strata. It is documented from the Heisdorf and Lauch Formations of the Eifel Hills, in horizons stratigraphically equivalent to the Eau Noire and Villers-la-Tour Members of the Ardennes, i.e. across the Emsian-Eifelian boundary (Birenheide *in* Werner and Ziegler 1982).

Lekanophyllum punctatum (Wedekind, 1924)
(Figs 14g–i)

* 1924 *Lekanophyllum punctatum*, Wedekind, p. 34, figs. 36–38.
p.p. 1964 *Plasmophyllum (Mesophyllum) auburgnese auburgense* (Wedekind, 1924); Bireheide, p. 36, pl. 4, fig. 14
? 1964 *Lekanophyllum* cf. *L. punctatum* Wedekind, 1924; McLaren and Norris, p. 22, pl. 8, figs 3–4
1969 *Cystiphylloides pseudomesophyllum*; Tsien, p. 90, pl. 2, fig. 7, pl. 42, fig. 4
2021 *Lekanophyllum punctatum* Wedekind, 1924; McLean, pl. 20, figs 7–9

Holotype: Specimen SMF WDKD2716-2720, figured by Wedekind (1924), figs 36–38, here illustrated as Fig. 14g.
Type locality and horizon: Southern side of Auburg Hill, Gerolstein Syncline, Eifel Hills, Eifelian Junkerberg Formation (Birenheide 1964).
Material: Four coralla from the Petigny Member (Cul d'Efer section).
Diagnosis (emended from Wedekind, 1924): Solitary cystimorph coral up to 35 mm in diameter, having up to 40 septa of each order, thin in the mature stage, usually divided into septal spines in the dissepimentarium. Tabularium poorly distinguishable from the dissepimentarium.
Description: Conico-cylindrical solitary coral, circular in transverse section, 20–30 mm in diameter with a poorly defined tabularium 11–18 mm in diameter (Fig. 15). Septa variously developed in inner dissepimentarium, divided into minor and major septa in some specimens (Fig. 14h), unrecognisable in others, 40–80 septa in total. Septa short, sinuous to tortuous, variable in length, interrupted by lonsdaleoid dissepiments and occasionally divided into isolated trabeculae. Dissepimentarium made of numerous rows of bulbous lonsdaleoid dissepiments and seldom concentric interseptal dissepiments. Wall 0.5 mm thick, straight and smooth. In longitudinal section, dissepiments and tabellae vesicular, irregular (Fig. 14i), scattered septal spines.

Discussion: Although slightly smaller than the type specimen, these corals display the development of septa and isolated trabeculae in the dissepimentarium typical of *Lekanophyllum punctatum* (Wedekind, 1924). It differs from other contemporaneous species such as *L. auburgense* (Wedekind, 1924) and *L. cylindricum* (Schlüter, 1882) by its larger diameter and longer septa.
Distribution: In the Ardennes, the species only occurs in the black fine-grained limestone of the Petigny Member. In the Eifel Hills, it extends through the upper Eifelian succession (Birenheide 1964). A very similar species (*L.* cf. *punctatum*) occurs in the Eifelian of NW Canada (McLaren and Norris 1964).

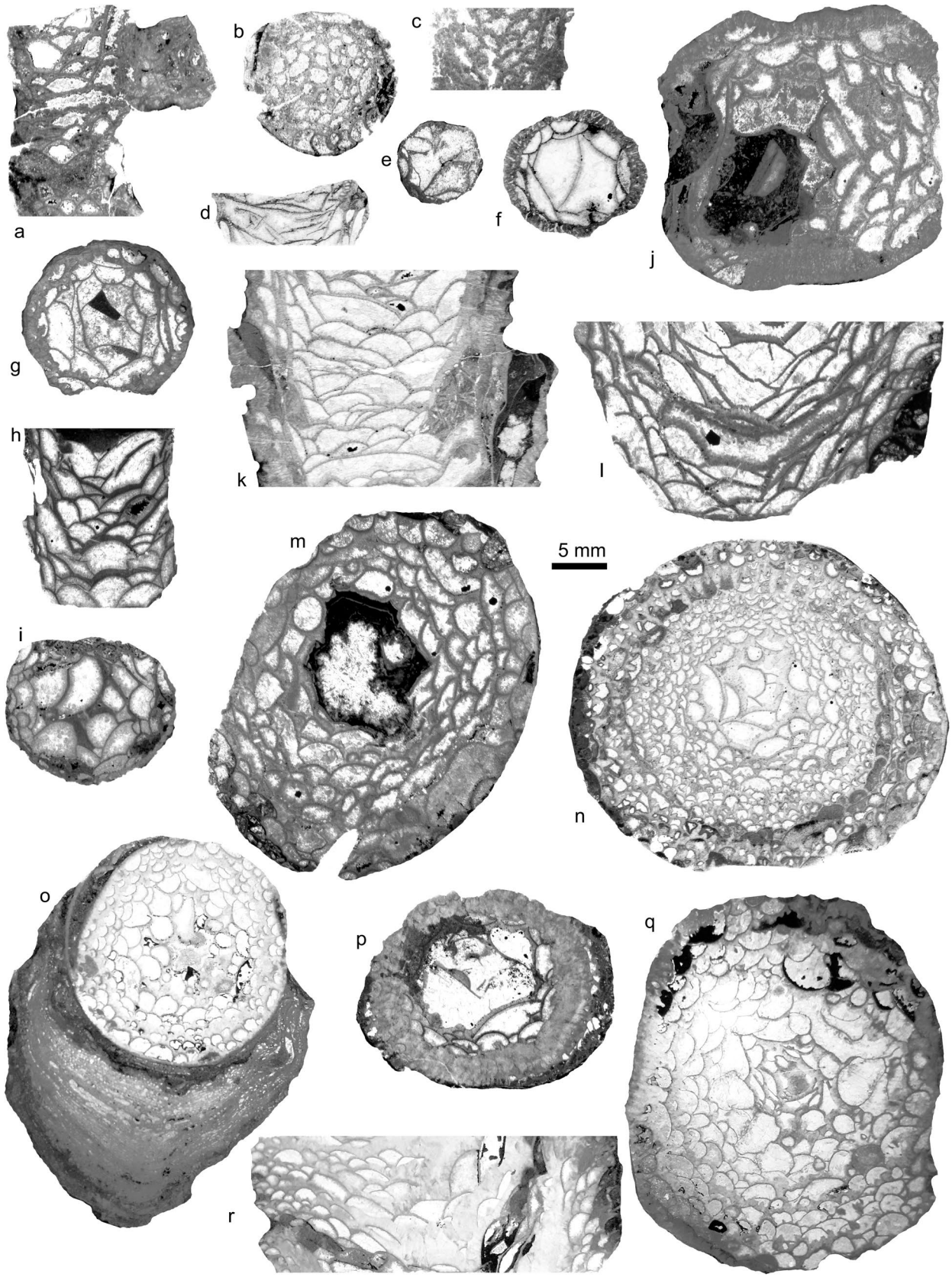
Digonophyllum Wedekind, 1923

Type-species: *Digonophyllum schulzi* Wedekind, 1923, from the lower Eifelian of the Eifel Hills.
Diagnosis: see McLean (2021).

Digonophyllum cf. *intermedium* (Vollbrecht, 1926)
(Figs 14p–r)

1969 *Mesophyllum arcuatum;* Tsien, p. 101, pl. 16, fig. 2a–b
1969 *Zonodigonophyllum primum* (Vollbrecht, 1926); Tsien, p. 104, pl. 21, figs 1–4
1969 *Zonodigonophyllum tenuis* (Vollbrecht, 1926); Tsien, p. 105, pl. 39, figs 1–3
1969 *Zonodigonophyllum tenuis* var. *tabulatum*; Tsien, p. 106, pl. 39, figs 4–5

Material: Three coralla from the lower part of the Villers-la-Tour Member (Villers-la-Tour and Eau Noire River sections) and one from the upper part of the Eau Noire Formation (Olloy section).
Description: Medium-sized cylindrical solitary coral 20 mm in diameter (Fig. 15), slightly elliptical in transverse section, with marked bilateral symmetry. Septa numerous, 38–40 of each order in mature stages, not carinate in the dissepimentarium. Major septa long, almost reaching the axis, straight in the tabularium and tortuous in the dissepimentarium, thickened in the cardinal quadrants of the tabularium (Fig. 14p). Minor septa long, contraclinant, interrupted in the periphery by lonsdaleoid dissepiments (Fig. 14r). Dissepimentarium made of 0–3 rows of small lonsdaleoid dissepiments and 3–5 rows of concentric interseptal dissepiments. Wall thin, usually eroded. In longitudinal section, dissepiments bulbous, inclined at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q
r

◂**Fig. 16** **a–c** *Microplasma caespitosum* (Schlüter, 1882), from the Eau Noire Member. **a** Specimen WZH-II/6-I, Halma section, in longitudinal section (LS). **b–c** Specimen WZH-II/11, Halma section, b in transverse section (TS), c in LS. **d–i** *Zonophyllum duplicatum* (Wedekind, 1924), from the Eau Noire Member. **d–e** Specimen W/30, Waha section, d in LS, e in TS. **f** Specimen W/31, Waha section, TS. **g** Specimen WZH-II/26-VII, Halma section, TS. **h–i** Specimen W/32, Waha section, h in LS, I in TS. **j–m** *Nardophyllum rosiforme* (Tsien, 1969) from the Eau Noire Member. **j–k** Specimen W/12, Waha section, j in TS, k in LS. **l–m** Neotype of *Nardophyllum rosiforme* (Tsien, 1969), specimen JG-I-B/6, Jemelle station section, l in LS, m in TS. **n–r** *Nardophyllum originale* (Birenheide, 1964) from the Eau Noire Member. **n** Specimen OTB/1, Olloy section, TS. **o** Specimen CEN-A/9, Eau Noire River section, TS. **p** Specimen CEN-A/6, Eau Noire River section, TS. **q** Specimen W/8, Waha section, TS. **r** Specimen CENA-10, Eau Noire River section, LS

45–60°. Tabularium incomplete, made of irregular vesicular and concave tabellae (Fig. 14r).

Discussion: The present material displays some characteristics of *Digonophyllum intermedium* (Vollbrecht, 1926): long thin septa not carinate, thickened in the tabularium, long minor septa, and a dissepimentarium with small lonsdaleoid dissepiments. However, it differs from Vollbrecht's species by its smaller diameter (up to 40 mm in the type material) and a tabularium better defined.

Distribution: In Belgium, these corals were collected in the basal Eifelian. *D. intermedium* comes from the lower Eifelian Nohn Formation of the Eifel Hills.

Digonophyllum perseptatum (Tsien, 1969)
(Figs 14b–f)

1969 *Hemicystiphyllum periseptatum*; Tsien, p. 92, pl. 14, figs 1–4, pl. 20, fig. 2, pl. 39, fig. 6a–b, pl. 41, figs 4–5

1969 *Hemicystiphyllum periseptatum* var. *tabulatum*; Tsien, p. 92, pl. 41, fig. 9a–b

*1969 *Hemicystiphyllum perseptatum*; Tsien, p. 93, pl. 41, figs 6–8, 10

1969 *Zonodigonophyllum primum* Vollbrecht, 1926; Tsien, p. 104, pl. 38, figs 6–8

Holotype: Specimen 3212 figured by Tsien (1969), pl. 44, fig. 1a–b.

Type locality and horizon: Left bank of the Eau Noire River in Couvin, uppermost part of the upper Emsian Eau Noire Member ('Co1c') (Tsien 1969).

Remark: From the same beds, Tsien (1969) erected the two species *Hemicystiphyllum perseptatum* and *H. periseptatum* which differ only in the thickening of the septa near the wall. This character, intrinsically variable in digonophyllids does not justify the distinction between two species. Although the original material is not well preserved, *H. perseptatum* is here selected as valid as the type specimen of *H. periseptatum* is lost.

Material: Five coralla from the upper part of the Eau Noire Member (Olloy and Halma sections), in addition to the type specimen of *H. perseptatum* Tsien (1969) from the Eau Noire River section.

Diagnosis (emended from Tsien 1969): Small solitary cystimorph coral < 15 mm in diameter with numerous septa well developed in the dissepimentarium, thin to thick. Large vesicular tabulae.

Description: Small cylindrical solitary coral 12–13 mm in diameter, with well-developed eccentric tabularium 8–9 mm in diameter (Fig. 15). Septa well developed but not separated into minor and major series, 50 septa in total, extending from the wall to the tabularium, slightly thickened and shorter in cardinal quadrants (Figs 14e–f). Dissepimentarium mostly composed of herringbone and angulo-concentric interseptal dissepiments, inner row usually thickened (Figs 14d, f). Wall up to 0.8 mm thick, smooth. In longitudinal section, dissepiments bulbous, relatively inclined. Tabellae vesicular, concave (Fig. 14b).

Discussion: With its small size, this species is very distinct from other *Digonophyllum* species. It differs from *Digonophyllum* cf. *intermedium* (Vollbrecht, 1926), which occurs in the same beds and has a similar size, by the development of the septa and a dissepimentarium more regular.

Distribution: *Digonophyllum perseptatum* (Tsien, 1969) has only been reported from the upper Emsian Eau Noire Member in the Ardennes.

Mesophyllum Schlüter, 1889

Type-species: *Actinocystis defecta* Schlüter, 1882, synonymised with *Cyathophyllum vesiculosum* Goldfuss, 1826 by Birenheide (1969), from the Middle Devonian of the Eifel Hills.

Remark: McLean (2021) considered *Mesophyllum*, based on the type-species *Cyathophyllum vesiculosum* Goldfuss, 1826, to be fasciculate and the equivalent in solitary morphology would be *Arcophyllum* Markov, 1926. However, the type species displays in the same beds both solitary and colonial morphology (Wedekind, 1925; Birenheide, 1964). Hence colonial and solitary corals are accommodated in *Mesophyllum*.

Diagnosis: See Pedder and McLean (1982).

Mesophyllum sp.
(Figs 14n–o)

1969 *Mesophyllum dubium* (Schulz, 1883); Tsien, p. 95, pl. 38, figs 11–12

Material: One corallum from the upper part of the Eau Noire Member (Waha section).

Description: Large cylindrical solitary coral 40 mm in diameter, tabularium 18 mm in diameter, having 47 septa of each order (Fig. 15). Major septa long, thin, sinuous,

with local thickening in the outer tabularium and dissepimentarium, slightly carinate. Bases of septa interrupted by lonsdaleoid dissepiments. Minor septa short, discontinuous, better developed in cardinal quadrants, interrupted by second-order lonsdaleoid dissepiments (Fig. 14m). Dissepimentarium made of 3–4 rows of irregular bulbous lonsdaleoid dissepiments and 10–15 rows of concentric and herringbone interseptal dissepiments, inner rows thickened. Cardinal fossula poorly conspicuous, open towards the declined axial part of the tabularium. In longitudinal section, dissepiments variable in size and shape, from small bulbous subhorizontal in periphery to elongated and declined at 45–60° in inner dissepimentarium (Fig. 14n). Tabularium made of irregularly spaced concave tabellae (11 tabellae per vertical centimetre), with a depressed axial part c. 6 mm in diametre. Septa appearing discontinuous vertically, with oblique trabeculae in the dissepimentarium.

Discussion: With its medium size, long and irregularly thickened major septa and short minor septa, this species is similar to *Mesophyllum laeve* (Schulz, 1883) but clearly differs from this Givetian species by its simpler dissepimentarium lacking dissepiments parallel to the septa. It is also very similar to *M. lissingense* (Schlüter, 1882) with its complex dissepimentarium and spindle-shaped septa but differs by the development of minor septa. Tsien (1969) figured a specimen from the Eau Noire Member under the name *Mesophyllum dubium* (Schulz, 1883) (synonym of *Lekanophyllum cylindricum* (Schlüter, 1882)) that is very similar to the present specimen but differs in having thinner and longer minor septa.

Distribution: Only known from the Eau Noire Member in the Waha section.

Subfamily Cystiphyllinae McCoy, 1851

Zonophyllum Wedekind, 1924

Type-species: *Zonophyllum duplicatum* Wedekind, 1924, from the lower Eifelian of the Eifel Hills.

Diagnosis: See McLean (2021).

Zonophyllum duplicatum Wedekind, 1924
(Figs 4q, 16d–i)

* 1924 *Zonopyllum duplicatum*; Wedekind, p. 14, figs 6–8
1924 *Legnophyllum cylindricum*; Wedekind, p. 13, fig. 5
? 1958 *Zonophyllum caducum* Wedekind, 1924; Bulvanker, p. 52, pl. 14, figs 1–3
1964 *Plasmophyllum (Plasmophyllum) antilimbatum* (Quenstedt, 1878); Birenheide, p. 21, pl. 4, figs 5–7, pl. 5, fig. 16, pl. 17, figs 82–83, pl. 18, figs 84–85, pl. 23, figs 107–108 [*cum. syn.*]
? 1969 *Cystiphylloides pseudoseptatum* (Schulz, 1883); Tsien, p. 78, pl. 19, fig. 1a–b
1969 *Cystiphylloides tabulatum* (Wedekind, 1924); Tsien, p. 79, pl. 19, fig. 1a–b, pl. 41, figs 1–2
non 1969 *Cystiphylloides duplicatum* (Wedekind, 1924); Tsien, p. 84, pl. 30, figs 14–17
? 1969 *Mesophyllum pseudocystiphylloides*; Tsien, p. 103, pl. 11, fig. 4a–c, pl. 25, fig. 2a–c
1978 *Mesophyllum (Cystiphylloides) duplicatum* (Wedekind, 1924); Birenheide, p. 176, fig. 111
1997 *Mesophyllum (Cystiphylloides) duplicatum* (Wedekind, 1924); Shröder, p. 19, pl. 4, figs 34–35
1998 *Mesophyllum (Cystiphylloides) duplicatum* (Wedekind, 1924); Shröder, p. 71, pl. 20, figs 113, 115

Lectotype: Specimen SMF 363 in Wedekind's collection, figured by Wedekind (1924), Fig. 8.

Type locality and horizon: Nohn, Hillesheim Syncline, Eifel Hills, Eifelian Nohn Formation (Schröder 1998).

Material: Four coralla from the Eau Noire Member (one from Halma, three from Waha).

Diagnosis: See Schröder (1998).

Description: Small sub-cylindrical to scolecoid solitary coral (Fig. 4p), 8-12 mm in diameter. Septal apparatus reduced to septal crusts and rare crests developed on the surface of external dissepiments and wall (Fig 16f–g). Dissepiments small and globose, arranged in vertical rows, passing to tabellae towards the axis, with no clear distinction between tabularium and dissepimentarium (Figs 16d–e). Tabellae vesicular, regular in size, sub-horizontal in the axial part. Stereoplasmic thickening occurs on some tabellae.

Discussion: This small species is easily distinguished from *Nardophyllum* spp. occurring in the same beds by its smaller diameter and the regularity of its tabularium.

Distribution: In the Ardennes, the species is only recorded from the upper part of the Eau Noire Member. In the Eifel Hills, it is known in the lower Eifelian Nohn Formation (Birenheide, 1964).

Microplasma Dybowski, 1874

Type-species: *Microplasma gotlandicum* Dybowski, 1874, from the upper Silurian of Gotland.

Diagnosis: See McLean (2021).

Microplasma caespitosum (Schlüter, 1882)
(Figs 4 j–k, 16 a–c)

* 1882 *Cystiphyllum caespitosum*; Schlüter, p. 209
p.p. 1969 *Cystiphylloides corneolum* (Wedekind and Vollbrecht, 1931); Tsien, p. 77, pl. 10, figs 1–2
p.p. 1969 *Cystiphylloides cylindricum* (Wedekind and Vollbrecht, 1931); Tsien, p. 81, pl. 23, figs 5–8
p.p. 1969 *Cystiphylloides duplicatum* (Wedekind, 1924); Tsien, p. 84, pl. 30, figs 14–17

1969 *Cystiphylloides primum* (Wedekind, 1924); Tsien, p. 104, pl. 30, fig. 13a–b
2021 *Microplasma caespitosum* (Schlüter, 1882); McLean, p. 45, pl. 12, figs 4–7, pl. 13, figs 1–3, 6 [*cum. syn.*]

Lectotype: Specimen GPIBo190a2, figured by Birenheide (1964), pl. 10, figs 51a–b.
Type locality and horizon: Ahütte, Hillesheim Syncline, Eifel Hills, Givetian Loogh Formation (Birenheide 1964).
Material: Tens of poorly preserved isolated corallites of small broken colonies from the upper part of the Eau Noire Member (Halma and Waha section).
Diagnosis: See McLean (2021).
Description: Weakly fasciculate colonies with lateral increase (Figs 4j–k). Small cylindrical corallites 11–15 mm in diameter. Septal crests very short, base embedded in the wall, forming a septotheca (Fig. 16b). Dissepiments vesicular to globular, not differentiated from tabellae (Figs 16a–c). No septal crusts but fibrous stereoplasmic deposits on dissepiments and tabellae.
Discussion: Most of the specimens consist of isolated branches but few display offsets suggesting that all these small-diameter corallites are indeed colonial. The thick septotheca and lack of septal elements on the dissepiments point therefore to the genus *Microplasma* rather than *Cystiphylloides*. Schröder (1998) revised the type material of *Cystiphylloides caespitosum* Schlüter (1882) and demonstrated its colonial morphology. The present material shares with the German species a similar size (12–15 mm in the type specimen) and a similar dissepimentarium composed of declined dissepiments near the wall and concave vesicular tabellae in the axial part. The most notable difference is the sub-cerioid morphlogy of the German material but this could be explained as an ecological adaptation.
Distribution: *Microplasma caespitosum* was described firstly from the lower Givetian Curten Formation of the Eifel Hills (Schröder, 1998). McLean (2021) recently discussed the synonyms of *M. caespitosum*, notably in China, Australia and North America. If the species is considered with a broad definition, then its stratigraphical extension covers the upper Pragian (e.g. in New South Wales, Hill 1942b), Emsian of the Ural Mountains (Soshkina 1949), Eifelian of Canada and China (Pedder 1980; Kong and Huang 1978) to the Givetian of Germany (Schröder 1998). In Belgium, the species has been collected in the upper part of the Eau Noire Member (Emsian-Eifelian boundary) and the Couvin Formation (Eifelian, unpublished data).

Nardophyllum Wedekind, 1925

Type-species: *Nardophyllum exzentricum* Borcher *in* Wedekind, 1925, from the lower Givetian of the Eifel Hills.
Diagnosis: See McLean (2021).

Nardophyllum rosiforme (Tsien, 1969)
(Figs 4b, o, 16j–m)

* 1969 *Cystiphylloides rosiforme*; Tsien, p. 90, pl. 17, figs 5a–c, pl. 18, fig. 5
p.p. 1969 *Cystiphylloides cuneiforme* (Wedekind, 1925); Tsien, p. 79, pl. 33, fig. 1
p.p. 1969 *Cystiphylloides corneolum* (Wedekind and Vollbrecht, 1931); Tsien, p. 77, pl. 30, fig. 7
? 1969 *Cystiphylloides pseudoseptatum* (Schulz, 1883); Tsien, p. 78, pl. 19, fig. 4

Neotype: The specimen 4435 from the Jemelle section, designated by Tsien (1969) and figured in his pl. 17, figs 5a–c is missing from the collection as well as the other syntypes. Hence, a lectotype cannot be chosen from the original collection, so the specimen JGI-B/6, from the type locality and type horizon, is designated as a neotype for the species.
Type locality and horizon: Jemelle station, Belgium, uppermost part of the upper Emsian Eau Noire Member ('Co1c') (Tsien 1969).
Material: Eleven coralla from the top of Eau Noire Member (three from Jemelle-station, including the neotype, and eight from Waha) and one from the Saint-Joseph Member (Treignes section).
Diagnosis (emended from Tsien 1969): Solitary cylindrical solitary cystimorph coral up to 30 mm in diameter, having small peripheral dissepiments and large irregular axial vesicular tabulae. Septal cones poorly marked.
Description: Large cylindrical solitary coral (Fig. 4b), circular to elliptical in transverse section, up to 30 mm in diameter. Septal crusts developed on wall and dissepiments, forming one or several septal cones in some specimens, but lacking in others, centred or slightly eccentric, vertically fused in juvenile stages (Figs 16j, m). Septal crests occur sporadically, protruding slightly out of the crusts (Fig. 16m). Dissepimentarium made of small globular dissepiments arranged in 1–4 strongly declined to vertical rows (Fig. 16h). Tabularium wide, made of irregular vesicular tabellae with general concave morphology (Fig. 16l). Tabellae irregularly spaced (6–8 tabellae per vertical centimetre).
Discussion: This large cystiphylline coral has a peculiar outer zone of small and packed dissepiments that is not characteristic of any other species but appears sporadically e.g. in *Nardophyllum secundum* (Goldfuss, 1826) and *N. cavanense* McLean, 2021. However, it differs from these species by a larger diameter, a narrower dissepimentarium and septal cones less developed.
Distribution: *Nardophyllum rosiforme* has only been collected in the Eau Noire Formation in Waha and Jemelle where it is particularly abundant.

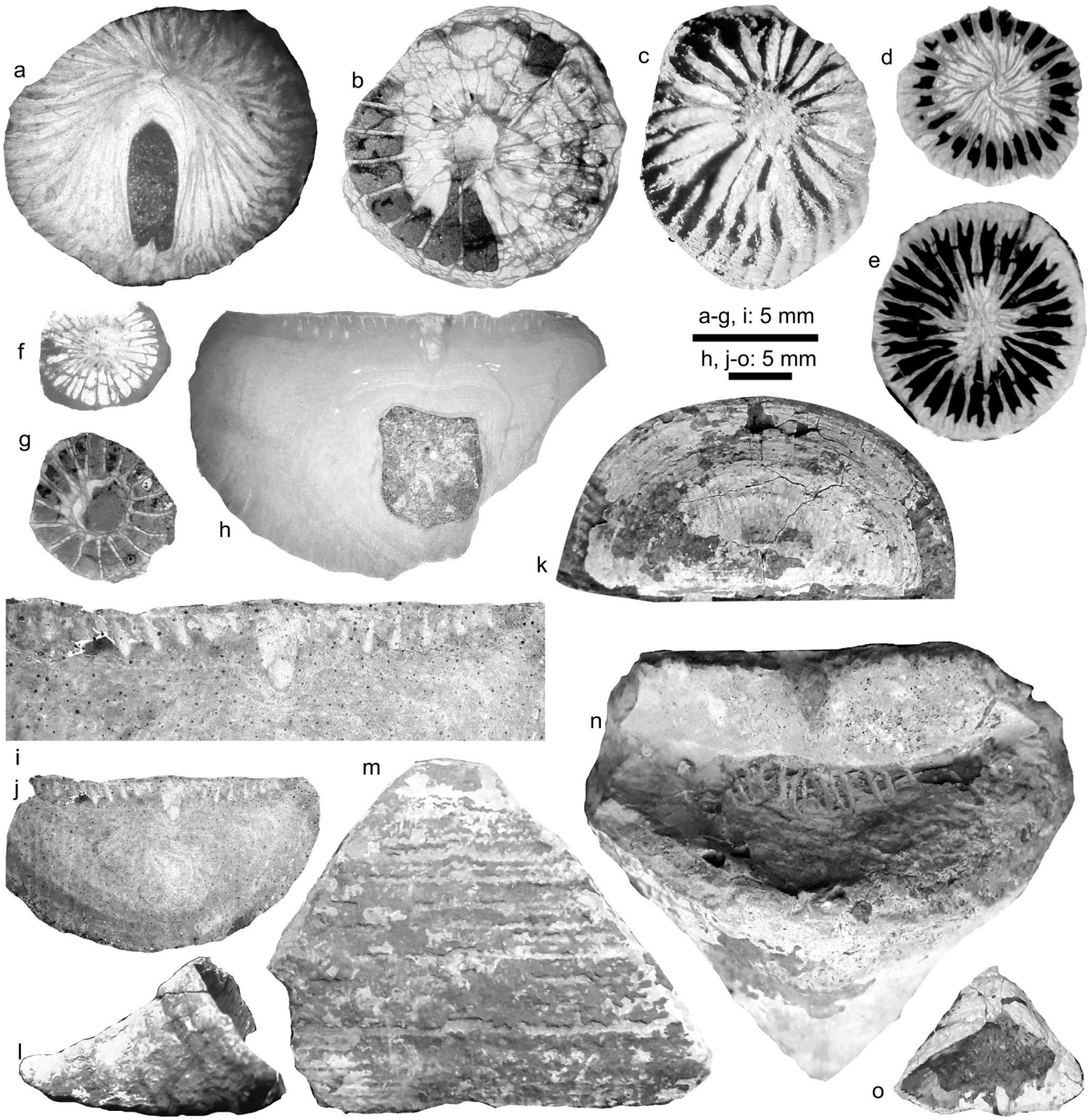

Fig. 17 **a** *Adradosia* cf. *barroisi* Birenheide and Soto, 1977, from the Vieux Moulin Member, specimen NAJ/1, Najauge section, transverse section (TS). **b–c** *Adradosia oolithica* (Frech, 1886), from the Vieux Moulin Member; 'Mur des Douanier'. **b** Specimen VIR/1, TS. **c** Specimen VIR/2, external vue of the steinkern. **d-e** Hapsiphyllidae? gen. et sp., from the Cimetière Member, specimen JR-II/2, Jemelle railway section, successive TS. **f** *Metriophyllum lituum* Holwell, 1964, from the Eau Noire Member, specimen W27, Waha section, TS. **g** *Neaxon* cf. *regularis* Kullmann, 1965, from the Saint-Joseph Member, specimen JG-I-A/1, TS. **h–o** *Calceola sandalina* (Linné, 1771), from the Eau Noire Member. **h–j** Specimen WZH/8, Halma section, successive TS. **i** Close-up view of j, x4. **k** Specimen WZH/13, Halma section, external view of the opercula. **l** Specimen W/55, Waha section, external lateral view. **m** specimen OTB/18, Olloy section, external view. **n** Specimen WZH/9, Halma section, external view. **o** Specimen WZH/10, Halma section, external view

Nardophyllum originale (Birenheide, 1964) *non* Kravtsov, 1966 (Figs 16n–r)

* 1964 *Plasmophyllum (Plasmophyllum) originale*; Birenheide, p. 23, pl. 3, fig. 1, pl. 18, fig. 88

p.p. 1969 *Cystiphylloides vermiforme* (Soshkina, 1952); Tsien, p. 85, pl. 10, figs 4–5

p.p. 1969 *Cystiphylloides corneolum* (Wedekind and Vollbrecht, 1931); Tsien, p. 77, pl. 11, figs 1–2

p.p. 1969 *Cystiphylloides tabulatum* (Wedekind, 1925); Tsien, p. 79, pl. 41, figs 1–2
p.p. 1969 *Cystiphylloides solidum* (Wedekind and Vollbrecht, 1931); Tsien, p. 80, pl. 31, fig. 2
p.p. 1969 *Cystiphylloides divisum* (Wedekind, 1925); Tsien, p. 83, pl. 31, figs 3-5
1978 *Mesophyllum (Cystiphylloides) originale* (Birenheide, 1964); Birenheide, p. 175, fig. 110

Holotype: Specimen SMF 15642, figured by Birenheide (1964), pl. 3, fig. 1.
Type locality and horizon: Dollendorf, Hillesheim Syncline, Eifel Hills, Emsian Heisdorf Formation (Birenheide 1964).
Material: Eight coralla form the Eau Noire Member (four from the Eau Noire River section, three from Olloy and one from Dion).
Diagnosis: See Bireheide (1964).
Description: Medium-sized cerato-cylindrical solitary coral, circular in transverse section, up to 22 mm in diameter. Tabularium and dissepimentarium poorly to not differentiated (Figs 16q-r). Septal crests developed on the wall and outer dissepiments (Figs 16p-q). Some crests form septa piercing 2–3 rows of dissepiments, usually more developed on one side of the corallum. Septal crusts developed in inner dissepimentarium, with smaller septal crests and stereoplasmic deposits on tabulae (Figs 15o-q). In longitudinal section, small globular dissepiments variably disposed, passing to vesicular tabellae connected by vertically fused septal crusts (Fig. 16r).
Discussion: *Nardophyllum originale* Birenheide (1964) differs from the other cystiphilline corals of similar diameter by the development of the septal crusts and the width of the dissepiments. The absence of packed dissepiments makes it different from *N. rosiforme* (Tsien, 1969).
Distribution: In the Ardennes, the species occurs in the upper part of the Eau Noire Member and the Saint-Joseph Member.

Familiy Hapsiphyllidae Grabau, 1928
Adradosia Birenheide and Soto, 1977

Type-species: *Adradosia barroisi* Birenheide and Soto, 1977 from the Emsian of the Cantabrian Mountains, Spain.
Diagnosis: See Weyer (1985).

Adradosia oolithica (Frech, 1886)
(Figs 4g, 17b–c)

*1886 *Zaphrentis oolithica*; Frech, p. 218, Pl. 13, fig. 25
? 1965 *Zaphrentoides (Hapsiphyllum) subguillieri*; Kullmann, p. 108, pl. 4, figs 7–8
? 1968 *Zaphrentoides (Hapsiphyllum) subguillieri* Kullmann, 1965; Kullmann, 1968, pl. 3, figs 8–9
1978 *Hapsiphyllum oolithicum* (Frech, 1886); Birenheide, p. 51, pl. 4, fig. 1
1996 *Adradosia? subguillieri* Kullmann, 1965; Soto and Kullmann, 1996, p. 662, pl. 81, figs 9–10
p.p. 2010 *Hapsiphyllum oolithicum* (Frech, 1886); Franke, 2010, p. 29, pl. 8, figs 1–5, pl. 9, figs 1–4, pl. 10, figs 1–7

Holotype: The specimen illustrated by Frech (1886), pl. 13, fig. 25, is lost and Birenheide (1978) indicated that the topotypic material is too poorly preserved to select a neotype.
Type locality and horizon: Rohr, Blankenheim Syncline, Eifel Hills, Emsian Heisdorf Formation (Birenheide 1978).
Material: One corallum from the 'Mur des Douaniers' locality near Vireux (plus five specimens preserved as mould of the calice, Fig. 17c) from the basal part of the Jemelle Formation and two coralla from Jemelle station section, one from the haematitic oolitic bed at the base of the Saint-Joseph Member and one from the Station Member.
Diagnosis: See Birenheide (1978).
Description: Conical corallum 7–9 mm in diameter, having 22–25 septa (Fig. 4g). Septa long and thin, reaching the axis, curved on both sides of the cardinal fossula (Fig. 17b). Cardinal major septum short. Minor septa not developed except the counter-lateral ones. Wall 0.4 mm thick, straight.
Discussion: Birenheide (1978) provided a description of this species based on topotypic material but included it in s *Hapsiphyllum* Simpson, 1900. Weyer (1985) demonstrated that hapsiphyllinae with coarse acanthine trabeculae should be included in *Adradosia* Birenheide and Soto, 1977. The species is however poorly known and requires a taxonomic revision. *Adradosia subguillieri* (Kullmann, 1965) is extremely similar and differs from *A. oolithicum* only by the absence of septal furrows on the outer surface of the wall (Birenheide 1978).

Adradosia cf. *barroisi* Birenheide and Soto, 1977
(Fig. 17a)

Material: One corallum from the Vieux Moulin Member (Najauje section).
Description: Solitary coral up to 13 mm in diameter, having 21 long major septa joined at the axis. Septa pinnately arranged on both sides of the cardinal fossula and radially arranged in the counter quadrants (Fig. 17a). Cardinal quadrants wider than counter quadrants. Cardinal fossula long, key-hole-shaped with withdrawn cardinal major septum.
Discussion: This single specimen differs from the type material of *Adradosia barroisi* Birenheide and Soto, 1977 by its more elongated fossula but the material is too scarce to provide a more convincing attribution.
Distribution: Lower part of the Eifelian (upper part of the Vieux Moulin Member of the Jemelle Formation).

Hapsiphyllidae? gen. et sp. indet.
(Figs 17d–e)

Material: One corallum from the Cimetiere Member (Jemelle-ravel section).
Description: Small solitary ceratoid coral up to 11 mm in diameter, having 25–30 septa of each order and a prominent axial structure up to 6 mm in diameter. Major septa slightly twisted at the axis in juvenile stages (Fig. 17d), more regular in mature stages (Fig. 17e). Minor septa long in mature stages. Cardinal and counter major septa connected, forming a plane of bilateral symmetry, except in more mature stages where all septa withdrawn from the axis and cardinal septum shorter. Wall straight and thick.

Family *Metriophyllidae* Hill, 1939
Metriophyllum Milne-Edwards and Haime, 1850

Type-species: *Metriophyllum bouchardi* Milne-Edwards and Haime, 1851, from the Frasnian of the Boulonnais area, France.
Diagnosis: See Holwill (1964).

Metriophyllum lituum Holwill, 1964
(Fig. 17f)

*1964 *Metriophyllum lituum*; Holwill, p. 116, figs 5–6, pl. 18, figs 2–4, 8
1969 *Metriophyllum lituum* Holwill, 1964; Tsien, p. 140, pl.1, fig. 5, pl. 5, fig. 6, pl. 29, fig. 5, pl. 37, fig. 4
1978 *Metriophyllum lituum* Holwill, 1964; Birenheide, p. 24, pl. 1, fig. 4
1992 *Metriophyllum lituum* Holwill, 1964; Birenheide and Soto, p. 104, pl. 3, fig. 15a–b

Holotype: Specimen MM11113 figured by Holwill (1964) pl. 18, figs 3–4, 8.
Type locality and horizon: Combe Martin Beach, South Devon, Givetian-Frasnian Ilfracombe Beds (Holwill 1964).
Material: Four coralla from the Eau Noire Member (Waha section).
Diagnosis: See Holwill (1964).
Description: Small ceratoid solitary coral 8–10 mm in diameter, having 28–32 septa. Major septa long and thin and, joined at the axis where they are slightly thickened, forming a slender axial structure. Cardinal septum straight, counter-lateral septa curved, bent towards narrow fossula. Minor septa forming small grooves embedded in the wall (Fig. 17f). Septal flanges expanding from the axis up to the middle of the tabularium, some reaching the wall. Wall up to 1 mm thick, undulating.
Discussion: With their thin major septa and undeveloped minor septa, these corals fit with the definition of *Metriophyllum lituum* Holwill, 1964 and therefore differ in those characteristics from *M. bouchardi* Milne-Edwards and Haime, 1850 which occurs in strata of similar age. *Metriophyllum skalense* Fedorowski, 1965 differs in having relatively long contratingent minor septa.
Distribution: *M. lituum* is documented from the Emsian of Belgium and the Givetian-Frasnian boundary beds of England (Holwill 1964) and Spain (Birenheide and Soto 1992).

Family *Laccophyllidae* Grabau, 1928
Neaxon Kullmann, 1965

Type-species: *Neaxon regularis* Kullmann, 1965, from the Emsian of the Cantabrian Mountains, Spain.
Diagnosis: See Kullmann (1965).

Neaxon cf. *regularis* Kullmann, 1965
(Fig. 17g)

Material: One corallum from the Saint-Joseph Member (Jemelle station section).
Description: Small solitary coral 4 mm in diameter, having 18 septa radially arranged and a prominent aulos 1.8 mm in diameter but not perfectly circular (Fig. 17g). Septa and wall thin.
Discussion: Size and morphology correspond to the described material of *Neaxon regularis* Kullmann, 1965 but the limited material does not allow further comparison.

Family Calceolidae King, 1846
Calceola Lamarck, 1799

Type-species: *Anomia sandalinum* Linné, 1771 from the Middle Devonian of the Eifel Hills.
Diagnosis: See Wright et al. (2010).

Calceola sandalina (Linné, 1771)
(Figs 17h–o)

* 1771 *Anomia sandalinum* Linné, p. 547
1969 *Calceola sandalina* forma *sandalina* (Linné, 1771); Tsien, p. 137, pl. 50, fig. 12, pl. 51, fig. 13–14, 17
1969 *Calceola sandalina* forma *alta* Richter, 1928; Tsien, p. 138, pl. 51, figs 15–16
1969 *Calceola sandalina* forma *angulatisima* Tsien; p. 139, pl. 51, figs 11–12
1998 *Calceola sandalina* (Linné, 1771); Pedder and Feist, p. 973, figs 6.1–6.6, 6.8, 6.10 [*cum. syn.*]
2010 *Calceola sandalina* (Linné, 1771); Wright et al., p. 124, figs 2–3
2020 *Calceola sandalina* (Linné, 1771); Jamart and Denayer, 2020, p. 293, fig. 7–I

Neotype: Specimen 1039a selected in Goldfuss'(1826) collection in the Goldfuss Museum in the Universität Bonn, figure 1 in Richter (1928).
Type locality and horizon: Eifel Hills, probably Eifelian.
Material: Sixteen coralla from the Eau Noire Member (12 from Halma, 3 from Waha, 1 from Olloy), only one in transverse thin section.
Diagnosis: See Wright et al. (2010).
Description: Typical calceolid morphology, dorso-ventrally compressed and curved growth axis (Fig. 17l). External counter surface finely striated transversally (probable growth ridges, Fig. 17m). On weathered specimens, longitudinal septal ridges appearing on counter side. Height (from tip to calice) 15–48 mm, length (larger size of calice) 16–52 mm and width (smaller size of calice) 8–25 mm. Apical angle varying from 55 to 80°. Dorsal side of the calice flat or convex, with a prominent septal tooth and up to 18 seplal ridges on both sides, some extending as very fine ridges fading away towards the apex in the inner part of the calice (Figs 17h–j). One single operculum preserved (Fig. 17k), semi-circular, 27 mm large and 13 mm wide, with concentric ridges on the cardinal edge and 42 (44?) fine radial ridges on internal side. Hinge part not preserved.
Discussion: As demonstrated by Wright (2006, 2007), the internal surface of the operculum bears diagnostic elements. As the only available operculum of the present collection only preserved the external surface, so its internal characteristics are unknown. Detailed discussions on calceolid corals are given in Pedder and Feist (1998) and Wright et al. (2010).
Distribution: *Calceola sandalina* is the typical marker of the former 'Couvinian' stage, extending from the uppermost Emsian to the lowermost Givetian. It is present in strata of that age across Europe, Asia and North Africa (see Pedder and Feist 1998 for review). In the Ardennes, the species is abundant in the Eau Noire Member, Jemelle Formation (mostly Chavées Member) and the Eifelian-Givetian Hanonet Formation (Wright et al. 2010), within argillaceous sediments. The species is much rarer in shallow-water limestone but occurs sporadically in the Couvin Formation.

Discussions

Emsian-Eifelian rugose coral faunas in North Western Europe

In North Western Europe, the Emsian depositional environment was usually unsuitable for the development of corals and only the uppermost Emsian yielded corals in Belgium and Germany, notably in the Eifel Hills.

Corals at the boundary between the Emsian and Eifelian were discussed by Birenheide (*in* Werner and Ziegler 1982) and Oekentorp and Brühl (1999), with a special focus on the Wetteldorf section, stratotype for the base of Middle Devonian. The upper part of the Heisdorf Formation and lower part of the Lauch Formation yielded *Adradosia* spp., *Kunthia* ex. gr. *crateriformis*, *Acanthophyllum vermiculare* and *A. radiatum*, *Nardophyllum* cf. *originale* (only from the Heisdorf Formation), *Zonophyllum duplicatum*, *Lekanophyllum cylindricum*, *Tabulophyllum lissingenensis* (only from the Heisdorf Formation) and *Calceola sandalina*. Additionally, the Wolfenbach Member of the Lauch Formation yielded *Xystriphyllum implicatum*, *Sociophyllum rolfwerneri* and *Mackenziephyllum* sp. The latter was described as an aphroid cystimorph coral by Birenheide (*in* Werner and Zielgler 1982) but a search in Birenheide's collection at the Senckenberg Institute was inconclusive and the specimen is supposed lost.

The occurrence of *Tabulophyllum lissingenensis* and *Nardophyllum originale* in the upper 15 m of the Heisdorf Formation (Birenheide *in* Werner and Ziegler 1982) allows a relatively obvious correlation with the upper 10 m of the Eau Noire Member of the Ardennes (Fig. 2). In both cases, the species are restricted to the Emsian part of the formations, i.e. below the base of the *partitus* conodont Zone. The disappearance of *T. lissingenensis* seems therefore to be a convenient marker for the Emsian-Eifelian boundary.

Localities in the eastern Rhenish Massif and the Harz also yielded undissepimented rugose, notably the Erbsloch Greywacke (Plusquellec and Jahnke 1999). Most of them require taxonomic revision before being used for correlations.

In Brittany (France), upper Emsian to lower Eifelian corals are reported from the *Calcaire de Chalonnes* of the Ancenis Syncline (Le Maître 1934), the *Calcaire d'Erbray* in the Angers Sycline (Barrois 1889), the *Schiste et Grauwacke de Run-ar-Chranc* in the Rade de Brest (Plusquellec and Semenoff 1972), and *Schiste des Marollières* in the Medio-Armorican Syncline (Plusquellec 1981). In each case, the rugose coral fauna contains of undissepimented solitary rugose corals, including the button-shaped Combophyllidae.

Emsian rugose corals were reported from the Carnic Alps, notably by Charlesworth (1914) but the precise age is usually not known and the specimens described are not figured. Flügel and Hubmann (1994) and Corradini et al. (2019) reported rugose corals from the lower Emsian Seewarte Formation and only *Tabulophyllum* sp. from the upper Emsian-lower Eifelian Vinz Formation.

In the Cantabrian Mountains in North Spain, the Moniello and Santa Lucia formations span the Emsian-Eifelian boundary and both display neritic carbonate facies with stromatoporoid and tabulate coral biostromes. The coral assemblage of the upper Emsian part of the Moniello Formation contains of *Acinophyllum* sp., *Adradosia subguilieri, Cayugea hispanica, Ceratophyllum* sp., *Combophyllum* sp., *Edaphophyllum sulcatum, Heliophyllum* sp., *Metriophyllum album*, *Nardophyllum originale*, *Petronella truncata*,

Prismatophyllum aff. *ovoideum*, *Pseudoamplexus* spp., *Stereolasma asturica*, *Ufimia prior* and *Xystriphyllum* sp. (Soto 1984). However, these corals are mostly known through faunal lists and their taxonomic attribution remains uncertain. More recently, Schröder and Soto (2003) and Soto and Schröder (2007) reported an endemic fauna composed of *Cantabriastrea cantabrica*, *Synaptophyllum multiseptatum* and *Tabulophyllum bonarense* from the Emsian part of the Moniello and Coladilla formations (slightly older, *serotinus* conodont Zone). The lower Eifelian part yielded *Acanthophyllum* cf. *vermiculare, Calceola sandalina, Cayugea hispanica*, *Combophyllum* cf. *lamellosum, Cystiphyloides monielloense, Edaphophyllum sulcatum, Metriophyllum album, Nardophyllum constrictum, Nardophyllum tabulatum, Stereolamsa asturica* and *Tabulophyllum lissingenensis* (Birenheide and Soto 1981; Soto 1984). Moreover, an assemblage dominated by undissepimented corals was reported by Kullmann (1965) and Soto and García-Alcalde (1976) from the Moniello Formation: *Adradosia endrissi*, A. cf. *simplex*, *A.* aff. *guillieri*, *Combophyllum* sp., *Homalophyllum* aff. *ungulum*, *Metriophyllum album, M. exiguum*, *Oligophyllum pentaphylloides, Petronella* sp., *Ufimia* spp. and many undetermined cystimorph rugosa (attributed to *Bucanophyllum, Cladionophyllum, Cystiphylloide*s and *Edaphophyllum* in Soto and García-Alcalde 1976).

The biostromes of the upper Emsian-lower Eifelian Santa Lucia Formation yielded a somewhat different fauna composed of *Acanthophyllum heterophyllum, Aulacophyllum* sp. *Breviphrentis* sp., *Calceola sandalina*, *Cayugea sp., Ceratophyllum* aff. *salmense, Chalcidophyllum gigas, Cystiphylloides ballonifer, C. monielloense, C. secundum, Embolophyllum aequiseptatum, Metriophyllum bouchardi, Nardophyllum macrocystis, Stringophyllum acanthicum* and *Tabulophyllum* sp. (Soto 1984; Fernández et al. 1995).

The Cantabrian Emsian-Eifelian corals are more diverse than the Belgian and German ones, with more colonial genera. The reason is probably linked to facies and to palaeolatitude, but the influence of the more diverse N American fauna is also marked, as demonstrated by the occurrence of the species of *Synaptophyllum, Cayugea, Edaphophyllum* and *Acinophyllum*.

In Montagne Noire (Southern France), the Emsian-Eifelian *Calcaire à polypiers siliceux* (Izarne Formation) yielded a very diverse rugose coral assemblage composed almost entirely of endemic species and genera (see detailed list in Pedder and Feist 1998). Schröder and Soto (2003) reported a single occurrence of *Synaptophyllum multiseptatum* near Cabrières in the Montagne Noire suggests a connection with the Spanish domain.

Emsian-Eifelian coral assemblages exist outside Western Europe, notably in the Ural Mountains (e.g. Bulvanker 1958; Tsyganko 1981) where the assemblages have taxonomic affinities with those of Western Europe. The North American (Pedder 2002; Pedder and Murphy 2003, 2004) and Australian (Hill 1942a, c; Pedder 1971; Zhen and Jell 1996, among others) coral faunas are characterised by a higher diversity and, in parallel, a higher endemism. Emsian fauna from Central Asia and China requires taxonomic reassessment and biostratigraphic control before being compared with corals of other provinces.

Rugose coral stratigraphy across the Early-Middle Devonian boundary

Rugose corals have been scarcely used for biostratigraphy in the Devonian because of supposed long extensions, endemism and taxonomic discrepancies. Such issues obviously exist but they are not more developed than in other groups, including the widely used conodonts. The biostratigraphic usefulness of corals is robust at the regional scale allows precise and accurate correlations between neighbouring basins and offers a pragmatic tool for the field.

In the traditional stratigraphic concept of the Western European Devonian, the 'Couvinian' stage was pragmatically defined by its coral fauna, with the base marked by the first occurrence of *Calceola sandalina*, cystimorph rugose corals and massive tabulate corals (Lecompte 1955). The increasing diversity from the base of the 'Couvinian' onwards can be used for biostratigraphy and correlations. Still, no significant change is observed across the boundary between the Emsian and Eifelian with the current conodont-based definition (Ziegler 2000). However, it seems that at least some taxa provide a useful stratigraphic signal.

Tabulophyllum lissingenensis and *T. tabulatum* first appear at two distinct horizons within the uppermost Emsian *patulus* Zone and both disappear almost at the boundary between the *patulus* and *partitus* Zones, i.e. at the boundary between the Emsian and Eifelian stages (Fig. 2).

Nardophyllum originale displays a very similar stratigraphic extension in Belgium (not known higher than the Eau Noire Member) but was recorded higher (base of Lauch Formation) in Germany (Birenheide 1964).

The first *Sociophyllum* species appear in Western Europe slightly above the base of the *partitus* Zone (base of Couvin Formation, i.e. < 5 m above the base of the stage in the Eau Noire River section) and in a similar horizon in the Wetteldorf section (Birenheide *in* Werner and Ziegler 1982) and Sauerland (Ernst et al. 2012).

The black dysoxic limestone that records the Choteč event in the Petigny Member of the Couvin Formation yielded only *Lekanophyllum punctatum*. The species first appeared in the Eifel Hills in the Lauch Formation and the Remsheid Formation in Sauerland (May and Avlar 1995) at a similar stratigraphic level. The Choteč event is recognised as the Dorsel Member of the Lauch Formation (Weddige 1988). Although the coral diversity dropped significantly during the deposition of this dark limestone, no extinction is

recorded and the coral species re-invested on the shelf after the event. The diversity increased progressively during the time corresponding to the deposition of the overlying Cul d'Efer and Abîme Members of the Couvin Formation and laterally-equivalent bioherm of the Wancennes Formation.

Conclusions

The revision of the rugose coral fauna in the upper Emsian-lower Eifelian of Belgium leads to the recognition of 27 species in 19 genera. The mostly Emsian Moulin de la Foulerie Formation, divided into a lower Saint-Joseph Member poor in corals and an upper Eau Noire Member, yields a diverse fauna of rugose corals. Among them, many large solitary corals include species of *Acanthophyllum* and *Nardophyllum*, associated with *Calceola*, *Tabulophyllum, Digonophyllum, Zonophyllum* and *Mesophyllum* as well as the smaller corals *Stringophyllum, Kunthia* and putative *Chostophyllum. Microplasma* is the first colonial genus recorded in the upper part of the Eau Noire Member. Undissepimented solitary corals are represented by *Neaxon* (in Saint-Joseph Member), *Metriphyllum* and *Adradosia*.

Although no major faunal change occurs across the Lower-Middle Devonian boundary, the extinction of *Tabulophyllum lissingenensis* and *Nardophyllum originale* are both almost coincident with the *patulus-partitus* conodont Zone boundaries.

The lower Eifelian Villers-la-Tour Member of the Couvin Formation yielded *Zonophyllum, Digonophyllum* and *Nardophyllum* but also *Grypophyllum* and the colonial genus *Sociophyllum*. The black limestone recording the Choteč event yielded a depauperate fauna with a single species of *Lekanophyllum*. Still, no extinction is associated with this horizon and the coral species re-appeared afterwards.

Correlations with the Eifel Hills are possible thanks to similar facies and coral associations but comparison with other Emsian fauna in Brittany, Cantabrian Mountains, Montagne Noire and Carnic Alps are hampered by a strong endemism.

Appendix 1

Sampled localities (see Fig. 1)

1. Villers-la-Tour disused railway (VTR): Villers-la-Tour Member of the Couvin Formation – 50°02'07"N 4°16'02"E.
2. Eau Noire River section in Couvin (CEN): continuous section exposing the Moulin de la Foulerie Formation and the lower part of the Villers-la-Tour Member of the Couvin Formation, see Tsien (1969) and Bultynck (1970) – from 50°02'34"N 4°29'53"E to 50°02'50"N 4°29'48"E.
3. Petigny Rue Augile section (CEIII): small disused quarry exposing the Petigny Member of the Couvin Formation and Cul d'Efer section (CEII) exposing the Villers-la-Tour Member of the Couvin Formation, see Denayer (2019) – 50°03'22"N 4°31'57"E, 50°03'12"N 4°31'38"E.
4. Olloy Tri-Baudet section along a forest path (OTB): natural section along a forest path exposing the upper part of the Eau Noire Member of the Moulin de la Foulerie Formation – 50°04'08"N 4°35'21"E.
5. Section along the Viroin in Treignes (TV): natural outcrop exposing parts of the Saint-Joseph and Eau Noire Members of the Moulin de la Foulerie Formation, see Denayer et al. (2015) – 50°05'16"N 4°40'07"E.
6. Najauge section E of Treignes (TN) and 'Mur des Douanier' (VIR) along the Vireux-Treignes road, both exposing the Vieux Moulin Member of the Jemelle Formation, see Dumoulin and Coen (2008) – 50°05'40"N 4°41'30"E and 50°05'38"N 4°42'18"E.
7. Dion 'Les Vérennes' (DiIII): small outcrops and blocks in ploughed crops exposing the Eau Noire Member and Sohier Beds – 50°06'47"N 4°52'56"E.
8. Wancennes (WPEIII): composite section exposing the base of the Wancennes Formation – from 50°05'47"N 4°57'50"E to 50°05'57"N 4°57'43"E.
9. Sohier (SN): disused small quarry along the road north of Sohier exposing the Sohier Beds and base of Vieux Moulin Member of the Jemelle Formation – 50°04'34"N 5°04'05"E.
10. Halma zoning section: vast temporary exposure during road works, exposing the top of the Eau Noire Member and the Sohier Beds of the Moulin de la Foulerie Formation – 50°04'56"N 5°07'42"E.
11. Grupont section (GRU): section along the road N803 and along the railway exposing the Eau Noire Member and Vieux Moulin Member, see Godefroid (1968) – 50°05'50"N 5°16'04"E.
12. Jemelle railway section (JR): long section along the disused Jemelle-Rochefort railway exposing the Station and Cimetière Members of the Jemelle Formation, see Maillieux (1913) and Godefroid (1968) – from 50°09'20"N 5°15'37"E to 50°09'13"N 5°14'39"E.
13. Jemelle station section (JG): long section along the road N849 exposing the Saint-Joseph and Eau Noire Members of the Moulin de la Foulerie Formation as well as the Station and Cimetière Members of the Jemelle Formation, see Godefroid (1968) – from 50°09'44"N 5°16'06"E to 50°09'26"N 5°15'58"E.
14. Waha (W) section: strongly weathered section exposing the Saint-Joseph and Eau Noire Members – 50°12'43"N 5°21'45"E.

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Data availability All material curated in the University of Liège is accessible to researchers (see also first paragraph of chapter "Systematic Palaeontology").

Declarations

Conflict of interest The author declares that he has no conflict of interest.

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