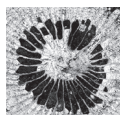# The Kačák event (late Eifelian, Middle Devonian) on the Belgian shelf and its effects on rugose coral palaeobiodiversity

Valentin Jamart & Julien Denayer

The Devonian is a period that recorded many biocrises. One of them, known as the Kačák event ranges through the *Polygnathus ensensis* Zone immediately before the Eifelian–Givetian boundary (Middle Devonian). This crisis has been identified in many localities worldwide, mostly in bathyal settings. The event, divided into two phases (*otomari* event and Kačák event *s.s.*), is typically marked by a turnover among pelagic faunas, especially conodonts, dacryoconarids and ammonoids. This turnover result from a transgression associated with anoxia that generally corresponds to the deposition of black shale in deep-water settings. In Belgium, the Kačák event *s.s.* corresponds to a time window equivalent to the deposition of the Lomme and Hanonet formations. New stratigraphic and palaeontological (rugose corals) data show that the Kačák event had a moderate to weak impact on the Belgian carbonate shelf ecosystem. The Old World Realm faunal assemblages show no significant variation in diversity across the Kačák event. Nevertheless, the remarkable and unexpected occurrence of some rugose corals typical of the East American Realm (siphonphrentids and heliophyllids) in the lower part of the Hanonet Formation helps identify the event as the latter is also marked by a short phase of cosmopolitanism of benthic fauna. This is a proposed criterion useful to recognize the Kačák event where the typical pelagic guides are missing. • Key words: biocrisis, extinctions, palaeobiogeography, stratigraphy, cosmopolitanism, invasive taxa.

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During the Devonian period, major continents/blocks were located in the southern hemisphere (*e.g.* Stampfli *et al.* 2002, 2013; Scotese 2014), with a major mountain range running on the northeastern margin of Laurussia to Gondwana: the Appalachian range (Fig. 1) (DeSantis 2010, Scotese 2014). This period of time is marked by one of the most significant modifications in palaeobiogeography with the precipitated end of the strong faunal endemism of the Emsian–Eifelian and the initiation of the Givetian–Frasnian cosmopolitanism (Oliver & Pedder 1979b).

During the early Emsian to late Eifelian interval, three distinct faunal assemblages allow the definition of three different marine realms (Oliver & Pedder 1979a, 1979b, 1994; May 1995, 1997b), separated by various barriers. The Malvinokaffric Realm (MKR), located along the margins of Gondwana (Fig. 1), is relatively poor in corals and it is characterized by cold-water species (Oliver 1990; Oliver & Pedder 1979a, 1979b, 1994; May 1995, 1997b). The East Americas Realm (EAR), located on the eastern part of North America and the northern part of South America (Fig. 1), is characterized by subtropical marine faunas and high degree of endemism (Oliver 1990; Oliver & Pedder 1979a, 1979b, 1994; May 1995, 1997b). The Old World Realm (OWR) covers the Palaeothetys Ocean and the margins of Laurussia, Kazakhstania and Siberia as well as the Chinese blocks and E Australian terranes (Fig. 1). It is also characterized by widespread subtropical marine faunas (Oliver 1990; Oliver & Pedder 1979a, 1979b, 1994; May, 1995, 1997b). The EAR is isolated from the OWR by a continental arch (Fig. 1) and the Appalachian mountain range (Oliver & Pedder 1979a; May 1995, 1997b).

Whereas the lowest sea level of the Devonian was recorded during the Emsian (May 1995, 1997b), the Middle Devonian recorded one transgressive pulse. This eustatic increase led to the collapse of the continental arch that separated the EAR from the OWR, and to the opening of a passageway allowing the migration of marine faunas between the two realms (Oliver & Pedder 1979a, DeSantis & Brett 2011). The faunal turnovers observed in the EAR are a probable consequence of this major

palaeobiogeographic change and most probably amplified the effects of the Kačák biocrisis (May 1995). Consequently, the end of the Eifelian stage was marked by both eustatic and palaeobiogeographic major changes (May 1995, Boucot *et al.* 1997, DeSantis & Brett 2011).

The Kačák event

During the Devonian, many biocrises have been identified (May 1995; House 1985, 1996). These crises are generally defined in bathyal settings, based on changes among pelagic faunas such as ammonoids and conodonts (Walliser 1996) but few or no extinction affecting the benthic faunas.

During the late Eifelian, the Kačák event (House 1985) is marked by faunal turnovers and by rapid facies changes, probably induced by a change of oxygenation in the water column in response to eustatic and/or temperatures variations (Chlupáč & Kukal 1986, DeSantis & Brett 2011). The Kačák event extended through the entire *ensensis* Zone directly below the Eifelian–Givetian boundary (House 1996, Walliser 1996, Schöne 1997).

This event was initially identified by the presence of anoxic black shale of the Kačák Member (Mb.) of the Srbsko Formation (Fm.) in the Barrandian area of Czech Republic (Chlupáč & Kukal 1986, 1988; Budil 1995; May 1995; House 1985, 1996). The black shale has a depleted fauna but ammonoids recovered from the units above the anoxic horizon differ significantly from those yielded by the level below the black shale (House 1985). Chlupáč & Kukal (1988) identified this horizon as an extinction event followed by a rapid radiation. Based on pelagic faunal changes, the event was subsequently identified in many localities worldwide, *e.g.* Rhenish Mountains in Germany (May 1995, House 1996, Schöne 1997, Königshof *et al.* 2016), Cantabrian zone and Asturian coast in Spain (Truyóls-Massoni *et al.* 1990, House 1996, García-Alcalde & Soto 1999, García-López *et al.* 2002), Scotland and SW England (House 1996, Marshall *et al.* 2007), Montagne Noire in France (House 1996), Carnic Alps in Austria (DeSantis & Brett 2011), Antiatlas in Morocco (House 1996, Becker *et al.* 2013), U.S.A. (DeSantis 2010, DeSantis & Brett 2011), Ontario province in Canada (van Hengstum & Gröcke 2008), Falkland Islands (Marshall 2016), Bolivia (Troth *et al.* 2011), Brasil (Horodyski *et al.* 2014), South China (House 1996, Qie *et al.* 2018), Australia (Talent *et al.* 1993, House 1996), and Vietnam (Königshof *et al.* 2017).

The Kačák event can be separated into two distinct phases spread over about 200 kyr (Walliser 1996, Schöne 1997, DeSantis 2010, Ellwood *et al.* 2011, Kido & Suttner 2011). The first phase – *otomari* event or *rouvillei* event or Ei 1 (in Walliser 1996) – corresponds to the base of the *ensensis* conodont Zone and is characterized by the

onset of anoxic black shales in many localities. It is also coincident with the boundary between the *kockelianus* and *ensensis* conodont zones and is associated to the spread of the dacryoconarid *Nowakia otomari* and the goniatite *Cabrieroceras crispiforme* (= *C. rouvillei* = *C. plebeiforme*) (House 1985; Chlupáč & Kukal 1986, 1988; Walliser 1996; Schöne 1997; DeSantis 2010; Ellwood *et al.* 2011). The black shale was deposited during a rapid rise of the sea level that triggered the abrupt development of anoxic conditions in the basin (Chlupáč & Kukal 1988). The second phase – Kačák event *s.s.* or Ei 2 (in Walliser 1996) – immediately before the Eifelian–Givetian boundary, is characterized by the end of the black shale deposition combined with numerous extinctions among goniatites (House 1996, Walliser 1996, Schöne 1997, DeSantis 2010, Ellwood *et al.* 2011). Marshall *et al.* (2007) suggested that a change in insolation could have triggered the event through an increase of temperature and consecutive stratification of oceanic water and development of anoxia transported towards the shelves by the correlative transgression (May 1995). The increase in precipitation (recorded as immature siliclastic deposits correlated with the Struve's "Great Gap", Struve 1982) would also have strongly decreased the salinity of seawater, eliminating the stenohaline organisms from the continental margins (May 1995, Marshall *et al.* 2007).

However, in basin settings, the sedimentary accumulation is slow and discontinuous and the resulting thickness is reduced, in the so-called condensed sections. Crises are there recorded as thin intervals and extinctions appear as abrupt events. It is the case for the Jebel Mech Irdane section (Moroccan Tafilalt) where the Kačák event is characterized by 0.5 m of anoxic black shales (Becker & House 1994, House 1996). In the Barrandian sections (Czech Republic) the event is marked by the abrupt onset of 0.5–3 m of anoxic black shales or equivalent (*e.g.* 'dark interval' in the Koněprusy area, Hladil & Kalvoda 1993, Budil 1995) associated with a faunal turnover (Chlupáč & Kukal 1986, 1988; Budil 1995; May 1995; House 1996). Conversely, in platform and ramp settings, the sedimentary accumulation is much higher, the sections are 'uncondensed' and the crises are often less well-marked due to the signal dilution. Extinction/turnover seems to be more gradual and lithological changes are more progressive. This dilution can nevertheless been regarded as a good opportunity to understand the succession of events within the event.

The development and effects of the Kačák event on shelves is not as well understood as those in bathyal settings. In the Rhenish Mountains, in neritic and hemipelagic facies, the Kačák event was identified in the Bonzel Fm.: the *otomari* event is recognized in the calcareous siltstones of the Bonzelhammer Mb. (lower part of the Bonzel Fm.) and the Kačák event *s.s.* corresponds to the

Figure 1. Evolution of land-masses and biogeographic realms in the Emsian (A), Eifelian (B) and Givetian (C). Legend & abbreviations: 1 – Carnic Alps; 2 – Prague Basin; 3 – Spain; 4 – Antiatlas; 5 – central North America; 6 – Scotland; 7 – Namur-Dinant Basin; 8 – Rhenish Mountains; 9 – Western Urals; 10 – South China blocks; 11 – Western Australia; 12 – Bolivia; 13 – Vietnam; 14 – Brazil; 15 – Falkland Islands; EAR – East Americas Realm; OWR – Old World Realm; Kz – Kazakhstania; NC – North China. Modified from Kido & Suttner (2011) and Scotese (2014).
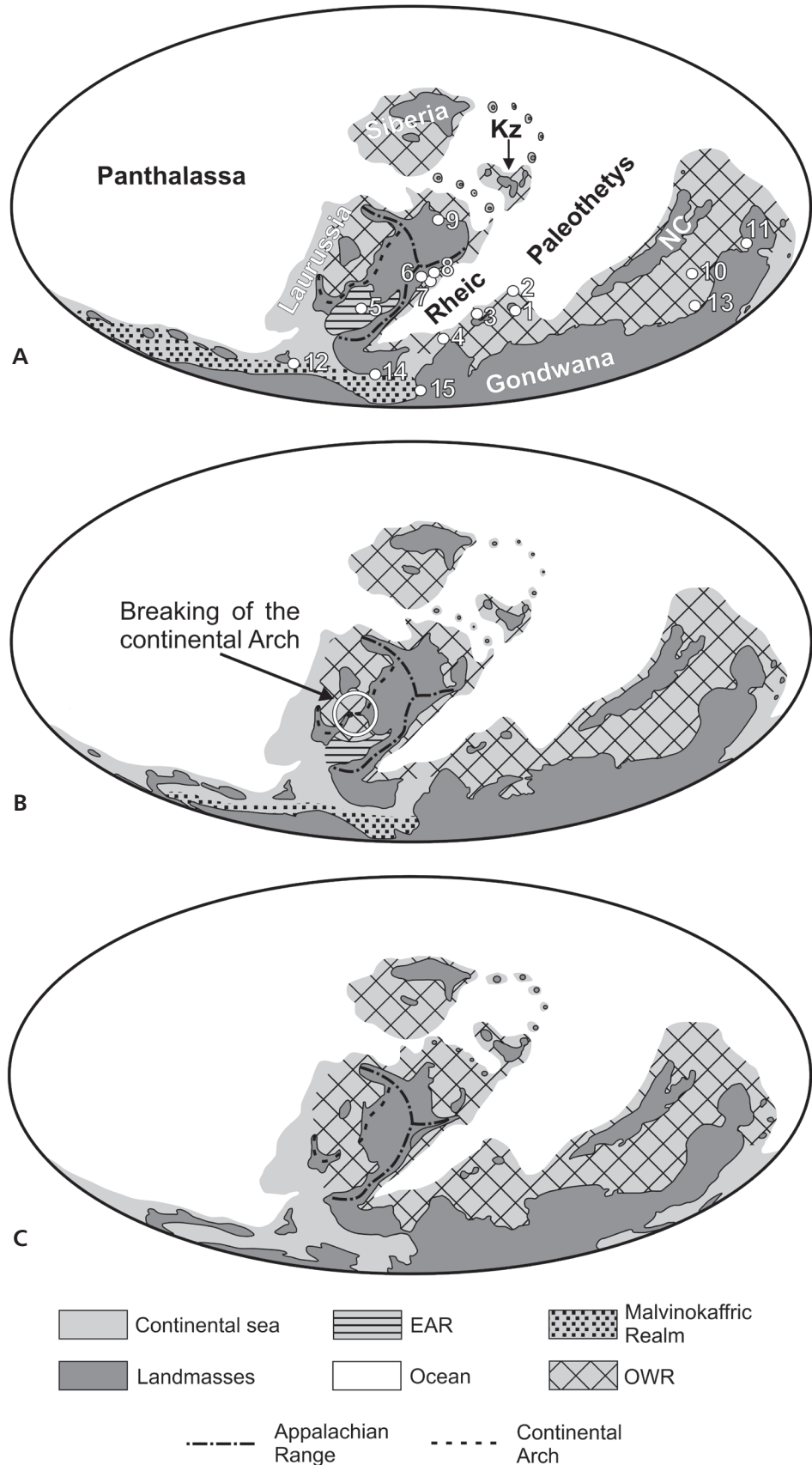
nodular limestone-bearing siltstone of the Senkel Mb. (upper part of the Bonzel Fm.) (Schöne 1997). In the Eifel, the event is marked by dark shale extending from the upper part of the Junkenberg Fm. (Giesdorf Mb.) to the lower part of the Freilingen Fm. (Eilenberg Mb.) (House 1996; May 1997a, b; DeSantis 2010). The onset of this shale coincides with a major δ^{13}C positive excursion (Königshof *et al.* 2016). This dark shale has a development of ~45 m (House 1996).

Gouwy & Bultynck (2003) suggested that in Belgium, the Kačák event corresponds to a 32 m-thick unit comprising the upper part of the Jemelle Fm. and the lower part of the Hanonet Fm. (see Geological and stratigraphic settings). However, biotic evidence for precisely placing the event was not provided convincingly by these authors. Based on ostracod diversity, Casier *et al.* (1992) indicated that there is no evidence for any anoxic phase associated to the Kačák event in the Hanonet Fm.

Faunal impacts of the event

As explained earlier, the Kačák event is associated with major changes in paleobiogeography, notably through the dismantlement of the MKR (May 1995, 1997a, 1997b; Walliser 1996; Boucot *et al.* 1997; Horodyski *et al.* 2014) and the replacement of mostly endemic EAR faunas by cosmopolitan taxa (Oliver 1990, Oliver & Pedder 1979a, May 1995). Even if major exchanges were mainly from the OWR towards the EAR, some invasions from the EAR towards the OWR were also identified (Schröder 1997b). Oliver & Pedder (1979b) suggested that the invading taxa coming from the OWR overwhelmed the EAR endemic taxa because the latter were less diverse and probably more adapted to quiet confined shallow water settings of E North America.

A significant loss of diversity was documented among anacerids (ammonoids) in the upper Eifelian before the

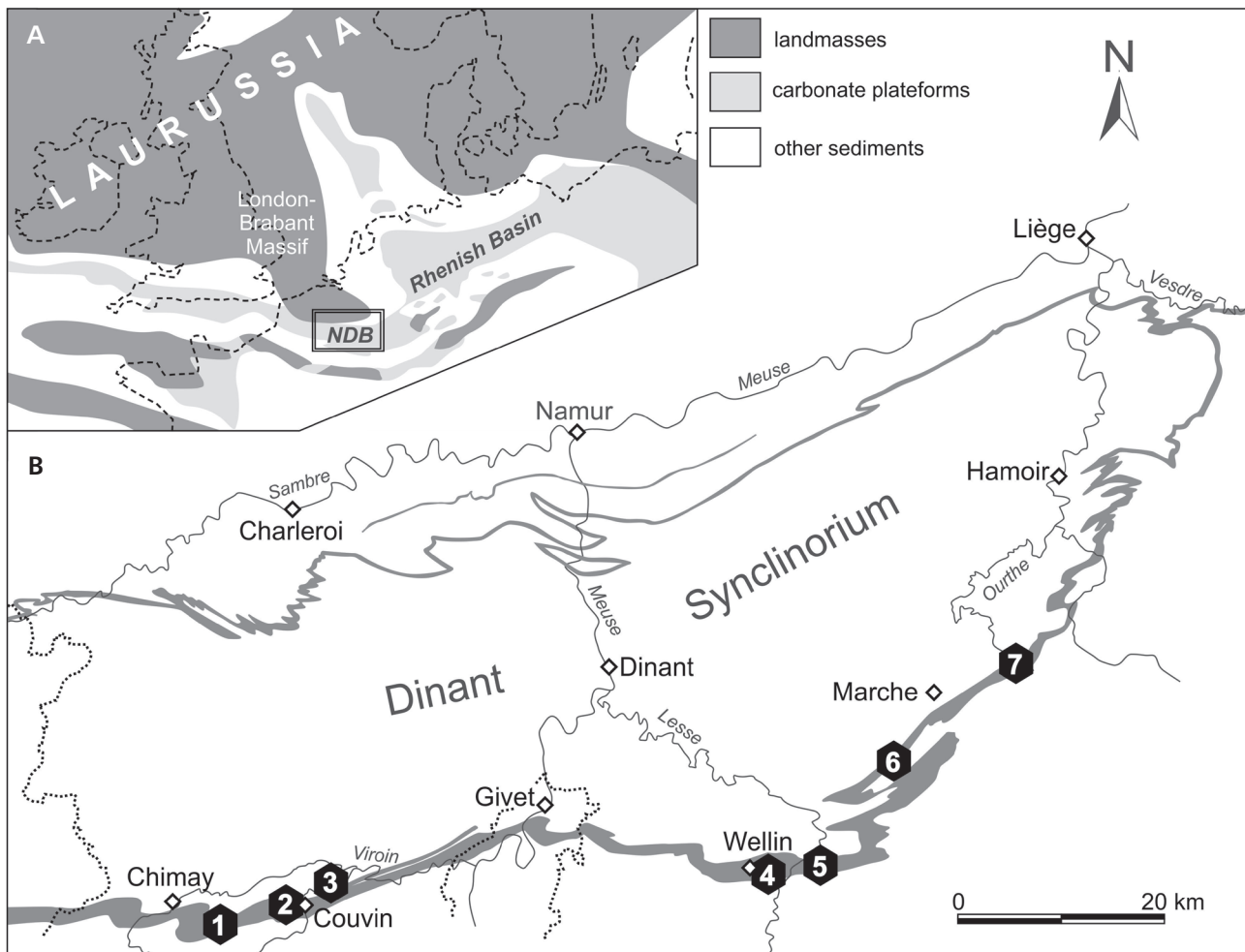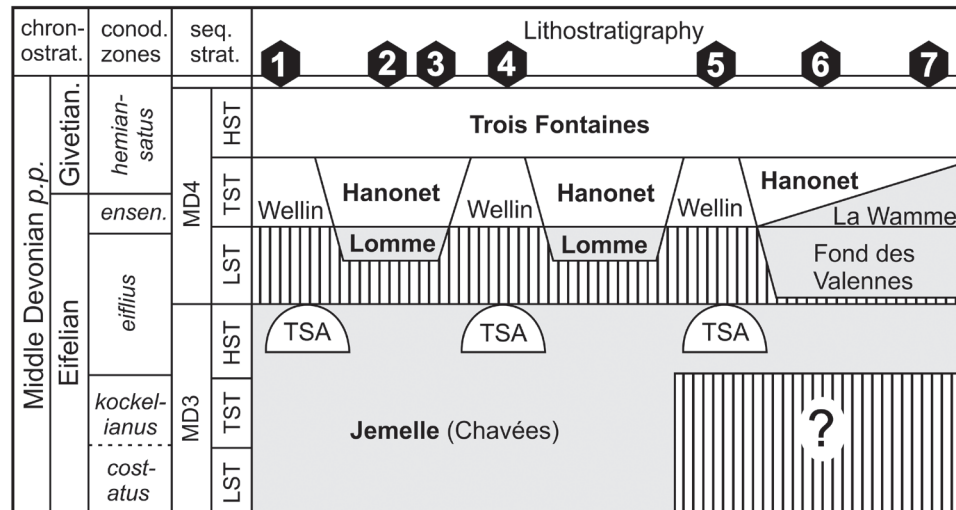**Figure 2.** Location and geological settings of the Namur-Dinant Basin. • A – palaeobiogeographic context of southern margin of Laurussia. • B – sampled localities along the southern margin of the Dinant Synclinorium. Legend: 1 – Baileux; 2 – Couvin; 3 – Nismes; 4 – Wellin; 5 – Resteigne; 6 – Jemelle; 7 – Hampteau. The Eifelian strata are represented by the grey line. Modified from Ziegler (1982) and Denayer (2019).

Figure 3. Stratigraphic chart for the upper Eifelian and the lower Givetian in southern Belgium. In Lithostratigraphy: formations names are in bold whereas the others are members. Legend & abbreviations: 1 – Baileux; 2 – Couvin; 3 – Nismes; 4 – Wellin; 5 – Resteigne; 6 – Jemelle; 7 – Hampteau; MD – Middle Devonian sequence; LST – lowstand system tract; TST – transgressive system tract; HST – highstand system tract; TSA – Tienne Sainte-Anne Member. Modified from Denayer (2019).

Descriptions

Geological and stratigraphic settings

During the Middle Devonian, the Namur-Dinant Basin of S Belgium corresponded to a shallow subtropical sea in the southern hemisphere along the southern coast of Laurussia (Fig. 2). From the Emsian to the Eifelian, a mixed carbonate and siliciclastic shelf developed and then evolved into a carbonate platform in the Givetian (Tsien 1969, Préat 1989, Préat & Kasimi 1995, Mamet & Préat 2005).

From SW to NE, the Namur-Dinant Basin shows a proximal-distal gradient (Kasimi & Préat 1996, Gouwy & Bultynck 2003). The Eifelian is well exposed in the Couvin and Wellin areas (~750 m) that correspond to the deepest part of the basin where continuous subsidence allowed a complete record (Kasimi & Préat 1996, Bultynck & Dejonghe 2001, Gouwy & Bultynck 2003). In the northern part of the basin, the thickness is significantly lower (up to 200 m in the Vesdre area) and the conglomerate-sandstone-siltstone succession recorded more proximal siliciclastic conditions (Bultynck 2006).

A short description of the lithostratigraphy is provided here. For further details, refer to Bultynck *et al.* (1991), Bultynck & Dejonghe (2001) and Denayer (2019).

The Jemelle Fm. (Fig. 3) is divided into several members (Bultynck *et al.* 1991), the upper one (Chavées Mb.) is dominated by shale and calcareous shale with limestone beds and nodules, rich in macrofauna (rugose and tabulate corals, brachiopods, bivalves and trilobites). Godefroid (1968) identified the brachiopod *Spinocyrtia ostiolata* in the lower part of the Chavées Mb. (*kockelianus* Zone). In Belgium, this species does not appear in the *ensensis* Zone, probably for facies reasons and therefore cannot be used as a marker of the Kačák event as it is in Germany

lower Givetian radiation of the tornoceratids (House 1985, DeSantis 2010, DeSantis & Brett 2011). Immediately before and during the event, a turnover is observed with several genera becoming extinct, whereas other radiates (*e.g. Agoniatites*, *Maenioceras*, *Cabrieroceras crispiforme*, *Holzapfeloceras* and *Wedkindella*) (House 1985, 1996; Chlupáč & Kukal 1986, 1988; Walliser 1996; Chlupáč *et al.* 2000; DeSantis 2010).

Turnovers were identified among conodonts with extinctions of many species of the genera *Polygnathus* and *Tortodus* (including *To. kockelianus*) and the radiation of *Icriodus* and polygnathidae such as *Po. ensensis* (Walliser 1996, Schöne 1997, DeSantis 2010, DeSantis & Brett 2011).

A similar pattern is observed with the dacryoconarids with the sudden appearance of *Nowakia otomari* as index taxa of the event and the disappearance of *N. chlupaciana* (Chlupáč & Kukal 1988, Budil 1995, Schöne 1997, Chlupáč *et al.* 2000, DeSantis & Brett 2011).

In the Rhenish Mountains, in Germany, May (1995, 1997a, 1997b) and Schöne (1997) suggested the link between the Kačák event and the appearance of two spiriferidae *Mucrospirifer diluvianus* and *Spinocyrtia* (*Spinocyrtia*) *ostiolata* known from older strata of EAR.

Beside the significant faunal exchange, the rugose coral diversity has yet been very poorly documented across the event. In Germany the event is marked by a change in the faunal assemblages of corals, from the upper Eifelian Freilingen and Ahbach formations to the lower Givetian; this complete change is not linked to an extinction but to the small decrease of Eifelian corals progressively replaced by Givetian taxa (Oliver & Pedder 1979a, Oliver 1990, May 1995, DeSantis 2010, Kido & Suttner 2011).

This paper aims to provide new clues to identify and understand the impact of the Kačák event on the Belgian shelf system, in particular on rugose corals.

(May 1995). In the upper part of the Chavées Mb., small bioherms (Tienne Sainte-Anne Mb.) locally develop (Bultynck 1970). The Jemelle Fm. reaches a thickness varying from 300 m (stratotype) to 600 m in the Wellin-Resteigne area (Bultynck *et al.* 1991). This formation belongs to the upper Eifelian *costatus* to *ensensis* biozones (Bultynck & Dejonghe 2001).

The Lomme Fm. (Fig. 3) is dominantly a more or less carbonate sandstone unit, arkosic in places where siltstone beds are not rare. This formation belongs to the upper Eifelian, *kockelianus* to *ensensis* biozones. It is stratigraphically equivalent to the upper part of the Jemelle Fm. and the lowermost part of the Hanonet Fm. (Bultynck & Dejonghe 2001). Denayer (2019) interpreted these silicoclastic deposits as the lowstand system tract of the Middle Devonian third-order sequence MD4. These deposits are well-developed in the eastern part of the Namur-Dinant Basin where the subsidence rate was apparently the highest (Godefroid 1968, Kasimi & Préat 1996). However siliciclastic deposits equivalent to the Lomme Fm. were reported in other places in the basin, notably in the Couvin area (Barchy & Marion 1999) where it seems to fill palaeodepressions between the highs formed by the underlying Tienne Sainte-Anne Mb. (Denayer 2019).

The Hanonet Fm. (Fig. 3) is typically made of thin beds of nodular, dark, argillaceous or slightly silty and micaceous limestone alternating with calcareous shale beds (Bultynck *et al.* 1991) passing progressively upwards to argillaceous limestone rich in brachiopods and corals. The thickness of the formation varies from 50 m in Couvin, to 70 m in Resteigne (Bultynck & Dejonghe 2001). In the stratotype of the formation in Couvin, Bultynck & Hollevoet (1999) identified the base of the Givetian 17 m above the base of the formation with the first occurrence of the conodont *Po. hemiansatus*. The Hanonet Fm. belongs to the upper Eifelian *ensensis* Zone and the lower part of the Givetian *hemiansatus* Zone. Denayer (2019) interpreted the Hanonet Fm. as the transgressive system tract of the Middle Devonian third-order sequence MD4, the middle argillaceous dark limestone unit being seen as the maximum flooding surface (or zone) of this sequence.

A peculiar facies contemporaneous with the typically argillaceous limestone of the Hanonet Fm. is recognized as the Wellin Mb. (Fig. 3). It is made of lenticular bodies of well-bedded crinoidal limestone, locally argillaceous, commonly rich in corals and stromatoporoids (Coen-Aubert *et al.* 1991). This member reaches a thickness of 115–120 m in the type locality (Bultynck *et al.* 1991, Bultynck & Dejonghe 2001). Laterally, the member shows a progressive transition from crinoidal grainstone to typical argillaceous wackestone-packstone of the Hanonet Fm. In Baileux and Nismes (Fig. 2), intermediate facies between Hanonet Fm. and Wellin Mb. are observed. The

Wellin Mb. is usually located immediately above the bioherms of the Tienne Sainte-Anne Mb. This is easily explained because these bioherms probably provided submarine relief which are more likely to be colonized by crinoids and stromatoporoids (Denayer 2019).

The Trois-Fontaines Fm. (Fig. 3) is divided into three parts. The lower one is made of few meters of thickly-bedded crinoidal limestone (Bultynck *et al.* 1991). The middle unit is characterized by biostromal limestone beds locally containing stringocephalid coquina beds (Bultynck *et al.* 1991). The depositional environment of this biostrome was abundantly described (Préat *et al.* 1984, Mamet & Préat 2005, Coen-Aubert 2008). This unit was interpreted by Denayer (2019) as the highstand system tract of the Middle Devonian MD4. The upper part of the formation is made of well-bedded micritic limestone (Bultynck *et al.* 1991). The later unit overlying a horizon with traces of emersion is interpreted as the lowstand and transgressive system tract of the next third-order sequence. Based on conodonts, this formation is entirely included in the lower Givetian *hemiansatus* Biozone (Bultynck & Dejonghe 2001).

Description of the sections

Five localities (Baileux, Couvin, Nismes, Resteigne and Jemelle) (Fig. 2, Appendix) located on the southern margin of the Dinant Synclinorium and exposing de Jemelle, Lomme, Hanonet and Trois-Fontaines formations were sampled. Data from the Hampteau and Wellin sections (Fig. 2) where the Wellin Mb. is exposed were included here but the lithological succession is very different and correlations with other sections are not easy (see Coen-Aubert *et al.* 1991). The typical facies of the Hanonet Fm. are exposed in the Couvin section (La Couvinoise quarry), Resteigne and Jemelle quarries sections. Based on these three sections, a composite lithological log was established. The resulting composite log displays a succession of eight lithological units in the Hanonet Fm.; these units are here described in ascending order.

Unit 1 (5 m-thick) overlies the transition from the Jemelle Fm. to basal Hanonet Fm. (Fig. 4). It is characterized by beds up to 20 cm-thick of bioclastic grainstone to packstone with crinoids, brachiopods and bryozoans and a small proportion of quartz grains. This unit is relatively poor in corals dominated by mud-stickers cylindrical forms such as *Acanthophyllum*, *Mesophyllum* and *Cystiphylloides*. The colonial *Thamnophyllum* is not uncommon but occurs commonly as fragmented colonies. This unit corresponds to the upper part of the Jemelle and Lomme Fm.

Unit 2 (13 m-thick) (Fig. 4) is characterized by alternation of dark argillaceous limestone in 20 cm-thick beds

and calcareous shaly interbeds up to 10 cm-thick whereas Unit 3 (9 m-thick) (Fig. 4) shows an increase in argillaceous content. These two units correspond to the lower part of the Hanonet Fm., even if the dark colour of these units could suggest a depletion of oxygen, the presence of an abundant benthic fauna (corals, brachiopods, ostracods, trilobites); the absence of anoxia facies-related taxa and the high degree of bioturbation are evidence for the absence of anoxia. The rugose coral assemblage is more diverse than in the previous unit, with several species of *Acanthophyllum*, *Aristophyllum luetti* Coen-Aubert, 1997, *Calceola sandalina* (Linnaeus, 1771), *Chostophyllum dollendorfense* Schröder, 1997, *Cyathopaedium paucitabulatum* (Schlüter, 1880), *Cystiphylloides* spp., *Enallophrentis martinae* (Coen-Aubert, 1996), *Glossophyllum ceratites* (Goldfuss, 1826), *Heliophyllum halleri* Schröder, 1995, *Mesophyllum* spp., *Spinophyllum incompositum* Schröder, 1997, *Stringophyllum acanthicum* (Frech, 1885), *Tryplasma rohrense* Glinski, 2001 and *Thamnophyllum* spp.

Unit 4 (Fig. 4) is characterized by a 20 m-thick regular alternation of argillaceous limestone and calcareous shale and corresponds to the middle part of the Hanonet Fm. It differs from the previous unit by its increasing carbonate content. The coral fauna of this unit is a depleted association with *Acanthophyllum* spp., *Aristophyllum luetti* Coen-Aubert, 1997, *Calceola sandalina* (Linnaeus, 1771), *Cyathopaedium paucitabulatum* (Schlüter, 1880), *Cystiphylloides* spp., ?*Grypophyllum* sp., *Macgeea bathycalyx* (Frech, 1886), *Mesophyllum* spp., *Microplasma* sp., *Stringophyllum* spp., *Tryplasma rohrense* Glinski, 2001 and *Thamnophyllum* spp.

Units 5 (15 m-thick) and 6 (18 m-thick) (upper part of the Hanonet Fm., Fig. 4) are similar in their lithological succession, each of them starts with few metres of more or less argillaceous bioclastic wackestone to packstone in which new faunas appear, then ends with argillaceous bioclastic and slightly bioturbated mudstone to wackestone. Locally (*e.g.* in Couvin, Fig. 4), thin biostromal beds with stromatoporoids and tabulate corals occur. They yielded the same rugose corals as the previous unit but also included *Chostophyllum dollendorfense* Schröder, 1997, *Cyathophyllum dianthus* Goldfuss, 1826, *Cystiphylloides macrocystis* (Schlüter, 1889), *Dohmophyllum* spp., *Grypophyllum* spp. and *Keriophyllum mailleuxi* (Tsien, 1969). In the uppermost part, Coen-Aubert (1990, 1996, 1998, 2011) reported *Sociophyllum torosum* (Schlüter, 1881), *Stringophyllum acanthicum* (Frech, 1885) and *Thamnophyllum* spp.

Unit 7 (15 m-thick, base of the Trois-Fontaines Fm., Fig. 4) is characterized by roughly stratified almost white crinoidal and bioclastic rudstone passing upwards to stromatoporoid and tabulate coral biostromes capped by stringocephalid coquina. Coen-Aubert (1988, 1990, 1992,

1996, 1997, 1998, 2008, 2011) abundantly documented the lower Givetian rugose coral association composed of *Acanthophyllum heterophyllum* (Milne-Edwards & Haime, 1851), *A. tortum* (Tsien, 1969), *A. vermiculare* (Goldfuss, 1826), *Beugnisastraea kunthi* (Schlüter, 1880), *B. parvistella* (Schlüter, 1882), "*Coenophyllum*" *groessensi* Coen-Aubert, 2008, *Columnaria intermedia* Coen-Aubert, 1990, *Fasciphyllum conglomeratum* (Schlüter, 1881), *F. katranicum* (Gorianov *in* Bulvanker *et al.*, 1968), *Keriophyllum mailleuxi* (Tsien, 1969), *Sociophyllum elongatum* (Schlüter, 1881), *S. torosum* (Schlüter, 1881), *Stringophyllum acanthicum* (Frech, 1885) and *Thamnophyllum occlusum* (Tsien, 1969).

The depositional environment and sedimentology of the Hanonet and Trois-Fontaines formations have been abundantly discussed (Casier & Préat 1990; Casier *et al.* 1992, 2016; Coen-Aubert 1996, 1997, 1998; Kasimi & Préat 1996; Mabille & Boulvain 2008). Kasimi & Préat (1996) summarized the evolution of the depositional environment as a progressive transition from outer ramp (upper part of Lomme and Jemelle Fm. and the base of the Hanonet Fm.) to median ramp (Hanonet Fm.) to outer platform (lower part of the Trois-Fontaines Fm.) and inner platform (upper part of the Trois-Fontaines Fm.). Local variations due to configuration of the basin (several tectonic blocks) demonstrate many exceptions to the depositional model. Moreover, it records a complete third-order sequence (Denayer 2019).

Distribution of the coral fauna

The Hanonet Formation is known to be homogeneous in lithology (mostly argillaceous limestone) but also to be very variable at the small scale (Kasimi & Préat 1996), with rapid lateral changes of facies notably in the Wellin Mb. (Denayer 2019). The faunal composition is also very variable from locality to locality as already mentioned by Coen-Aubert (1996, 1997, 1998) and Godefroid (1995). However, the background faunal composition of the formation is rather uniform, dominated by various species among the genera *Acanthophyllum*, *Cystiphylloides*, *Mesophyllum* and *Calceola*.

In the upper Eifelian and lowermost Givetian part of the Hanonet Fm. (unit 2 to 4), there is no significant variation in rugose corals diversity, with the notable exception of the co-occurrence of uncommon taxa such as *Aristophyllum* (occurring from unit 2 and disappearing in unit 6), *Enallophrentis* and *Heliophyllum* (both restricted to units 2 and 3). Other common corals are *Acanthophyllum*, *Calceola*, *Chostophyllum*, *Cyathopaedium* (not found above the unit 4), *Cystiphylloides*, *Glossophyllum* (only found in the unit 3), ?*Grypophyllum* (found from unit 4 to unit 6), *Macgeea* (found from unit 4 to 6), *Mesophyllum*,

Spinophyllum (only found in the unit 2), *Tryplasma* and *Thamnophyllum*. The dimensions and development of some long-ranging species (both cystimorphic and septate solitary rugose corals) show no significant change throughout this interval, suggesting a relatively stable environment.

In the Wellin Mb. of the Hanonet Fm., the peculiar crinoidal limestone and associated facies yielded a rather different fauna, including numerous colonial genera such as *Cyathophyllum*, *Dendrostella*, *Fasciphyllum*, *Lyrelasma*, *Neomphyma*, *Sociophyllum*, *Thamnophyllum* and *Xystriphyllum* (Coen-Aubert 1989, 1990, 1992; Coen-Aubert *et al.* 1991).

In the Givetian part of the formation (unit 5 and 6), a slight decrease of diversity is observed, with the disappearance of some corals such as *Aristophyllum*, *Calceola* (not found in unit 6), *Chostophyllum*, *Cyathophyllum*, *Cystiphylloides*, *Dohmophyllum* (appearing in the unit 5 and disappearing in the unit 6), *Grypophyllum* (found only in unit 5 and 6), *Macgeea*, *Mesophyllum* (not found in unit 6), with the appearance of new taxa such as *Sociophyllum* and *Keriophyllum* in unit 5. The major shift occurs right after the boundary between the Hanonet and Trois-Fontaines formations (unit 7 and 8), with the local disappearance of the genera *Acanthophyllum*, *Cystiphylloides*, *Sociophyllum* (except that *S. birenheidi* and *S. torosum* are known in the lower part of the Trois-Fontaines Fm.), *Stringophyllum* and with the total disappearance of other genera such as *Thamnophyllum* and the uncommon *Keriophyllum* which do not occur above the lower part of the Trois-Fontaines Fm. This change is coincident with the shift from ramp settings to platform settings that probably led to the displacement of these opportunistic faunas. In addition the base of the Trois-Fontaines Fm. recorded the appearance of new taxa such as *Beugnisastraea*, *Columnaria* and *Centristella* (Coen-Aubert 1988, 1990, 1997) and the development of new species among the genera *Sociophyllum*, *Disphyllum* and *Thamnophyllum* (decribed by Coen-Aubert 1988, 2008).

Apart from these two small changes (turnovers rather than extinctions) near the Eifelian–Givetian boundary and at the Hanonet–Trois-Fontaines transition, rugose and tabulate corals seem not to have been severely affected. The main diversity changes are mostly related to changes in facies. In conclusion, neither coral diversity nor their disparity seems to have changed significantly during the interval corresponding to the Kačák event.

Beside corals, the brachiopod fauna of the Hanonet Fm. was documented by Godefroid (1995), the ostracods were documented by Casier & Préat (1990) and Casier *et al.* (1992, 2016), the trilobites by Van Viersen (2007) and Crönier & Van Viersen (2007) and the conodonts by Bultynck (1970) and Bultynck & Hollevoet (1999).

Systematic palaeontology

The rugose coral fauna of the upper Eifelian to lower Givetian Hanonet and equivalent formations were, in part, described by Coen-Aubert (1992, 1996, 1997, 1998, 2000), Coen-Aubert & Lütte (1990), Coen-Aubert *et al.* (1991) and Tsien (1969, except for the type material, all Tsien's specimens are lost). Coen-Aubert (1988, 1992, 1996, 1997, 1998, 2000) documented in details the following species, hence they will not be re-described here: *Sociophyllum torosum* (Schlüter, 1881), *Neomphyma dalcqae* Coen-Aubert, 1992, *Keriophyllum mailleuxi* (Tsien, 1969), *Acanthophyllum vermiculare* (Goldfuss, 1826), *A. heterophyllum* (Milne-Edwards & Haime, 1851) and *Aristophyllum luetti* Coen-Aubert, 1997, *Thamnophyllum occlusum* (Tsien, 1969) and *Grypophyllum* cf. *denckmanni* Wedekind, 1922. Additional information on taxonomy and stratigraphy can be found therein. Moreover, *Calceola sandalina* (Linnaeus, 1771) was described and discussed by Wright *et al.* (2010). From the Wellin Mb. ('Formation X' in Coen-Aubert *et al.* 1991) in its type-locality, Coen-Aubert (1989, 1990, 1992) described *Xystriphyllum pachythecum* (Glinski, 1955), *Cyathophyllum multicarinatum* Coen-Aubert, 1989, *Fasciphyllum conglomeratum* (Schlüter, 1881), *Neomphyma delicata* Coen-Aubert, 1990, *Stringophyllum wadilinum* Coen-Aubert, 1989, *Lyrelasma mutabilis* (Tsyganko, 1977), *Sociophyllum semiseptatum* (Schlüter, 1881) and *S. rolfwerneri* (Birenheide, 1979). Some of them are figured in the present paper (*e.g.* the common genus *Acanthophyllum* in Fig. 5).The presently described material is reposited in the Palaeontological Collection of the University of Liège.

Class Anthozoa Ehrenberg, 1834
Subclass Rugosa Milne-Edwards & Haime, 1850
Order Stauriida Verrill, 1865
Family Zaphrentidae Milne-Edwards & Haime, 1850

Genus *Heliophyllum* Hall *in* Dana, 1846b

Type species. – *Heliophyllum halli* Milne-Edwards & Haime, 1850.

Diagnosis. – See Oliver & Sorauf (2002).

***Heliophyllum halleri* Schröder, 1995**
Figure 6A, B

> *1995a *Heliophyllum* (*Heliophyllum*) *halleri* n. sp.; Schröder, p. 40, pl. 1, figs 6, 7, pl. 2, figs 8–10, pl. 3, figs 11, 12, text-figs 4, 5.
> 1995b *Heliophyllum* (*Heliophyllum*) *halleri* n. sp. – Schröder, p. 386, pl. 2, figs 10–13.
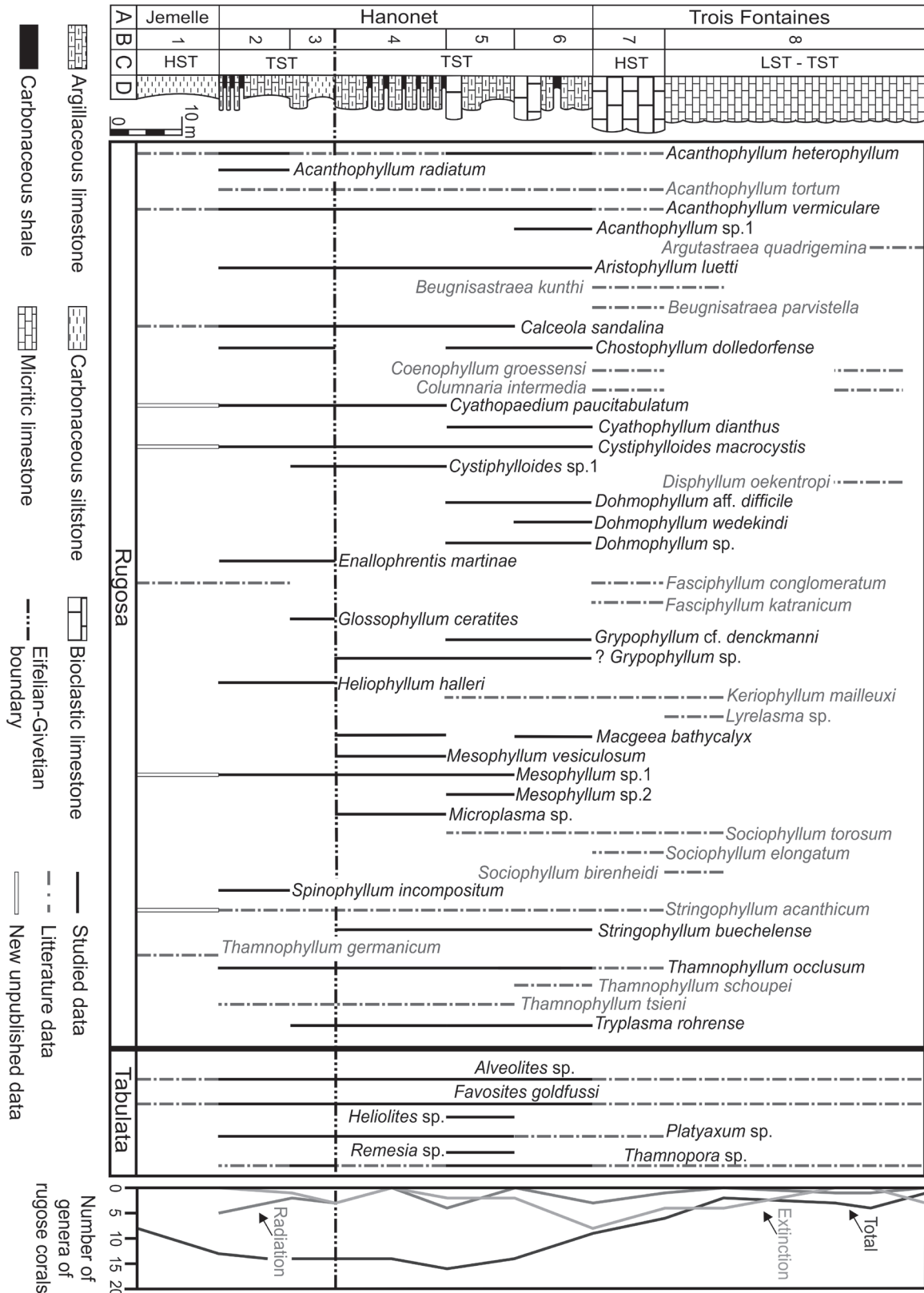
Figure 4. Stratigraphic distribution of rugose and some tabulate corals in the Jemelle, Hanonet and Trois-Fontaines formations. Legend: A – litho-stratigraphy; B – lithological units; C – sequence stratigraphy; D – lithology; HST – highstand system tract; LST – lowstand system tract; TST – transgressive system tract. Literature data comes from Coen-Aubert (1988, 1990, 1992, 1996, 1997, 1998, 2008, 2011) and Boulvain *et al.* (2011).

1996 *Rhytidolasma dahlmense* (Haller, 1936). – Coen-Aubert, p. 26, pl. 1, fig. 8, pl. 3, figs 1–5, pl. 4, figs 1–7.
1997a *Heliophyllum* (*Heliophyllum*) *halleri* Schröder, 1995. – Schröder, p. 10, pl. 2, fig. 14.
1998 *Heliophyllum* (*Heliophyllum*) *halleri* Schröder, 1995. – Schröder, pp. 30, 31, pl. 2, figs 9, 10.

Material. – Resteigne (RES/2015.09.29/1).

Diagnosis. – See Schröder (1995a).

Description. – Specimens with 38 septa of both orders at a diameter of 37 mm. The major septa are long but do not reach the axis of the corallum and leave a free space. The major and the minor septa are thin, bearing well-marked yardarm carinae. The minor septa are ¾ as long as the length of the major septa. The dissepimentarium comprises 16–17 rows of regular dissepiments, the outer one or two rows possess a concavity orientated outwards, in the other rows the concavity is orientated towards the axis of the corallum. There is an open, shallow cardinal fossula (Fig. 6A). The width of the tabularium is 17 mm. In longitudinal section, the dissepiments are horizontal in periphery and declined towards the axis at an angle of 70° (Fig. 6B). The tabulae are incomplete. There is 15 tabulae/cm.

Discussion. – This specimen is similar to those attributed to *H. halleri* Schröder, 1995 by Schröder (1995a, b, 1997a, 1998). It differs from *H. dahlmense* (Haller, 1936) by a clearly-marked recognizable fossula and a larger dissepimentarium. Moreover, the septa of *H. halleri* bear almost exclusively yardarm carinae whereas *H. dahlmense* possessed zigzag carinae (Schröder, 1995a). The thickening is more frequent, not only restricted to the center of the corallum, which clearly distinguishes this material from *H. halli* Milne-Edwards & Haime (1850). The characters observed by Coen-Aubert (1996) in her material from Resteigne (30–47 septa of both orders, diameter of 20 to 46 mm, septa more or less thickened in the dissepimentarium, major septa usually reaching the axis of the corallum, tabulae incomplete, minor septa just entering into the tabularium, some being contratingents, 21 to 26 rows of dissepiments, tabularium 9.7 to 23 mm) are typically diagnostic for *H. halleri* as suggested by Schröder (1995a) and *H. dahlmense* sensu Birenheide (1963). Hence, we consider the Belgian material to belong to *H. halleri* rather than *H. dahlmense*.

Occurrence. – The specimen comes from the disused Resteigne quarry, from the lower part of the Hanonet Fm., in the *ensensis* Zone. This species is known from the upper Eifelian Freilingen Fm. of the Eifel Mountains (Schröder 1995a, b, 1997a, 1998).

Genus *Chostophyllum* Pedder, 1982

Type species. – *Chostophyllum metula* Pedder, 1982.

Diagnosis. – See Schröder (1997a).

***Chostophyllum dollendorfense* Schröder, 1997**
Figure 6F–H

*1997a *Chostophyllum dollendorfense* n. sp.; Schröder, p. 13, pl. 2, figs 20–24, text-figs 3–5.
1998 *Chostophyllum dollendorfense* Schröder, 1997. – Schröder, p. 39, pl. 8, fig. 52.
2014b *Chostophyllum* cf. *dollendorfense* Schröder, 1997. – Abbasi *et al.*, p. 129, figs 5c, d.

*Material.* – Resteigne (RES I-3/12 éb., RES I-9/8, RES I-11/3, RES II-5/15, RES II-5/6 éb.).

Diagnosis. – See Schröder (1997a).

Description. – Specimens with 26 to 30 septa of both orders at a diameter of 11 mm to 19 mm. The major septa almost reach the centre of the corallum but leave a free space. The septa are bent towards the cardinal fossula (Fig. 6F). The septa are commonly thickend in the tabularium. The minor septa are half as long as the length of the major septa. The dissepimentarium comprises 2 to 7 rows (5 on average) of regular dissepiments. The width of the tabularium is of 7.5 mm to 11.6 mm. The external wall is thick, particularly in juvenile stages. In longitudinal section, the tabulae are complete, flat and evenly distributed vertically (8 tabulae/cm).

Discussion. – The specimens are identical to those attributed to the material described by Schröder (1997a, 1998) and also to the material from N Iran described by Abbasi *et al.* (2014b).

Occurrence. – This species is common in the whole Hanonet Fm. on both sides of the Eifelian–Givetian boundary, in Resteigne. This species is known from the upper Eifelian

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Figure 5. Ptenophyllids rugose corals from the Hanonet Formation. • A–C – *Acanthophyllum vermiculare* (Goldfuss, 1826), specimen COUV I-6/3 from Couvin, TS (A) and LS (B), specimen RES I-7/2 éb. from Resteigne, TS (C). • D – *Acanthophyllum radiatum* (Wedekind, 1924), specimen RES I-3/13 éb. from Resteigne, TS. • E, F – *Acanthophyllum heterophyllum* (Milne Edwards & Haime, 1851), specimen COUV I-4/7 from Resteigne, TS (E), specimen JML-M/1 from Jemelle, TS (F). • G, H – *Acanthophyllum* sp.1, specimen COUV I-6/12 from Couvin, TS (G) in a juvenile stage and TS (H) in a mature stage. Magnification ×2 for all specimens.

1 cm
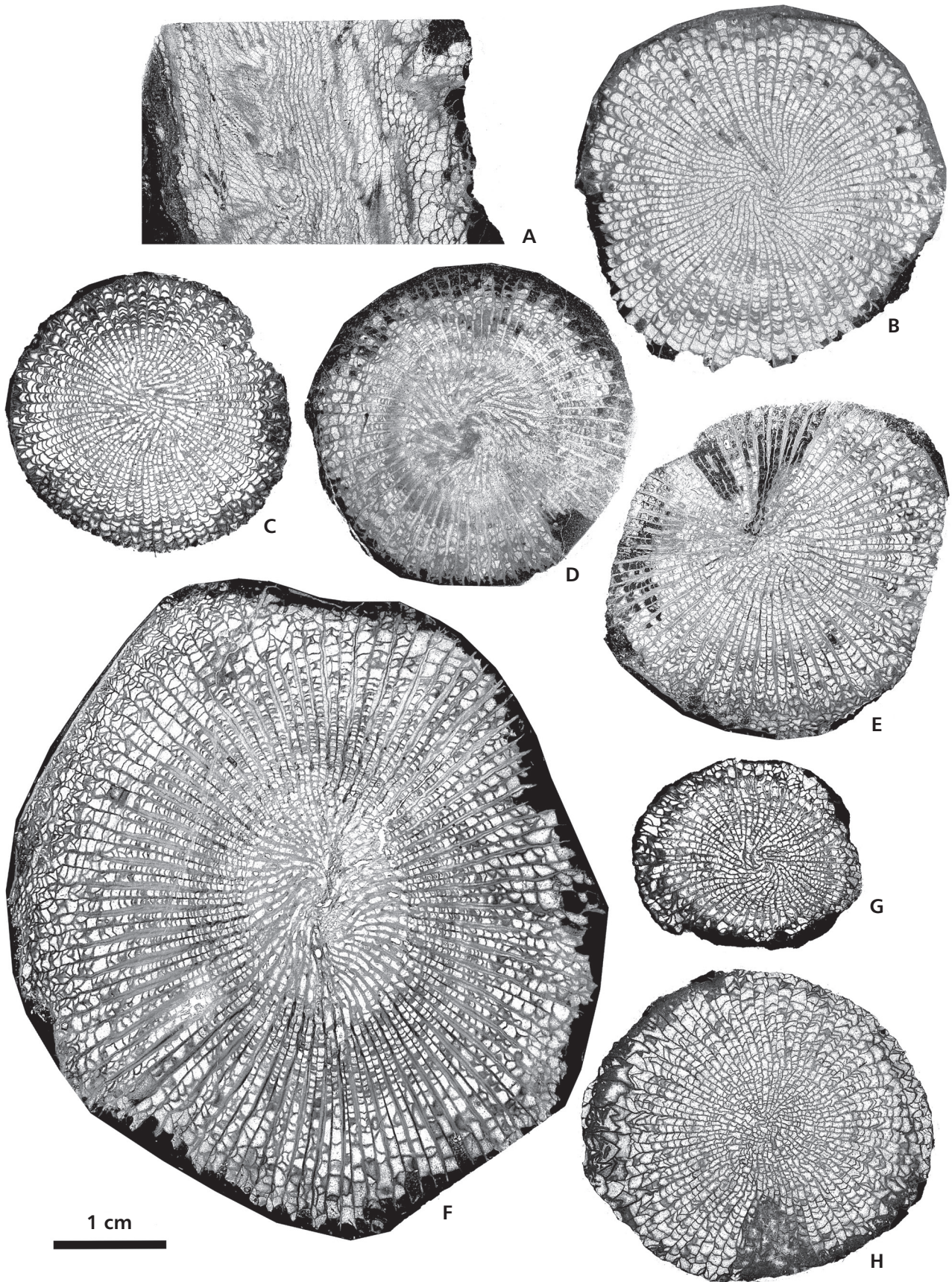
of the Eifel Mountains (Freilingen Fm.; Schröder 1997a, 1998) and the Givetian of Iran (Abbasi *et al.* 2014b).

Family Cyathopyllidae Dana, 1846a

Genus *Glossophyllum* Wedekind, 1924

Type species. – *Glossophyllum dohmi* Wedekind, 1924.

Diagnosis. – See Hill (1981).

Glossophyllum ceratites (Goldfuss, 1826)
Figure 6E

  *1826 *Cyatophyllum ceratites* nobis; Goldfuss, p. 57, pl. 17, fig. 2i.
   1987 *Glossophyllum ceratites* – Lütte, p. 441, pl. 4, figs 16, 17, pl. 5, figs 18–22, pl. 6, figs 24, 25, pl. 7, fig. 28. [*cum syn.*]
  ? 1998 *Glossophyllum* sp. cf. *ceratites* (Goldfuss, 1826). – Schröder, pp. 32, 33, pl. 3, fig. 12.
   1999 *Glossophyllum ceratites* (Goldfuss, 1826). – Schröder & Kazmierczak, p. 99, pl. 2, fig. 6.
   2014a *Glossophyllum ceratites* (Goldfuss, 1826). – Abbasi *et al.*, pp. 12, 13, pl. 2, fig. 5.

Material. – Resteigne (RES II-5/4 éb.).

Diagnosis. – See Birenheide (1978).

Description. – Specimen having 38 septa of both orders at a diameter of 26 mm. The major and the minor septa are of a similar thickness (Fig. 6E). The major septa are long but do not reach the axis of the corallum and leave a free space. The minor septa are ¾ as long as the major septa and cross the entire dissepimentarium. The wall is slightly thickened. The dissepimentarium comprises 7–8 rows of regular concentric dissepiments. The tabularium is 16 mm-wide.

Discussion. – This single specimen fits the definition of *G. ceratites* and is very similar to the specimens attributed to *Ceratophyllum ceratites* by Tsien (1969), Birenheide (1978), Lütte (1987), Schröder (1998), Schröder & Kazmierczak (1999) and Abbasi *et al.* (2014a); see Schröder (1998) for further discussion on this species.

Occurrence. – The specimen comes from the lower part of the Hanonet Fm. (*ensensis* Zone) in the Resteigne section. This species is known from the upper Eifelian to the lower Givetian of the Eifel Mountains (Freilingen, Loogh and Cürten formations) (Birenheide 1978, Lütte 1987, Schröder 1998). Outside Europe, this species has been identified in the lower Givetian of Eastern Albroz Mountains (Kosheyilagh Formation) in NE Iran (Abbasi *et al.* 2014a) and Morocco (Ouihalane "coral reef", E Anti-Atlas, Schröder & Kazmierczak 1999).

Genus *Spinophyllum* Wedekind, 1922

Type species. – *Campophyllum spongiosum* Schlüter, 1889.

Diagnosis. – See Hill (1981).

Spinophyllum incompositum Schröder, 1997
Figure 6C, D

  *1997a *Spinophyllum incompositum* n. sp.; Schröder, p. 9, pl. 1, figs 6–13.
   1998 *Spinophyllum incompositum* Schröder, 1997. – Schröder, p. 37, pl. 4, figs 30, 31.

Material. – Resteigne (RES I-3/5 éb., RES I-3/14 éb.).

Diagnosis. – See Schröder (1997a).

Description. – Specimens with 30 to 33 septa of both orders at a diameter of 16 mm to 22 mm. The septa are commonly carinate and spindle-shaped thickened in the dissepimentarium and thinner in the the tabularium (Fig. 6C). The major septa are long but do not reach the axis of the corallum and leave a free space in the centre. The minor septa are half as long as the major septa and they are restricted to the dissepimentarium. The wall is thickened. The dissepimentarium includes 5 to 8 rows of regular dissepiments, the inner row being thickenend by a stereoplasmic deposit. The width of the tabularium varies from 8.2 mm to 11.5 mm.

Discussion. – The specimens are similar to the type material described by Schröder (1997a, 1998).

Figure 6. Heliophyllid, siphonophrentid and cyathophyllid rugose corals from the Hanonet Formation. • A, B – *Heliophyllum halleri* Schröder, 1995, specimen RES/20150929/1 from Resteigne [A in longitudinal section (LS), B in transverse section (TS)]. • C, D – *Spinophyllum imcompositum* Schröder, 1997, specimen RES I-3/5 éb. from Resteigne, TS (C), specimen RES II-9/17 from Resteigne, TS (D). • E – *Glossophyllum ceratites* (Goldfuss, 1826), specimen RES II-5/4 éb. from Resteigne TS. • F–H – *Chostophyllum dollendorfense* Schröder, 1997, specimen RES I-3/12 éb. from Resteigne, TS (F), specimen RES I-9/8 from Resteigne, TS (G), specimen RES I-11/3 from Resteigne, TS (H). • I, J – *Cyathophyllum dianthus* (Goldfuss, 1826), specimen 2015.10.13/09 from Couvin TS (I-J); I – transverse section showing offsets. Magnification ×2 for all specimens.
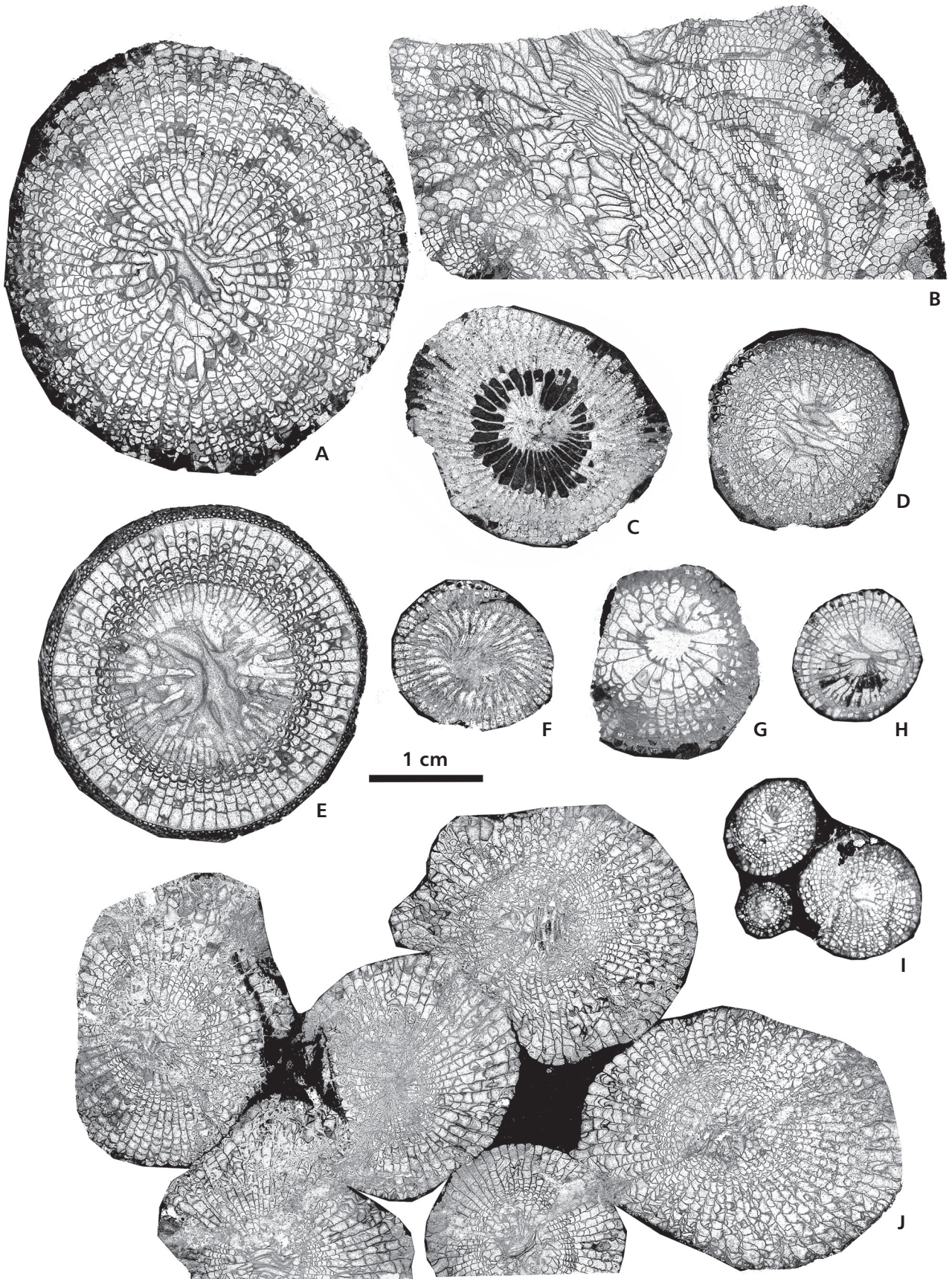
Occurrence. – The specimens come from the lower part of the Hanonet Fm. (*ensensis* Zone) of Resteigne. This species is known from the upper Eifelian Eilenberg Mb. (lower part of the Freilingen Fm.) in the Eifel Mountains and, more generally, from the upper Eifelian to Givetian of Eurasia (Schröder 1997a, 1998).

Family Siphonophrentidae Merriam, 1974a

Genus *Enallophrentis* Oliver, 1993

Type species. – *Strombodes simplex* Hall, 1843.

Diagnosis. – See Oliver (1993).

Enallophrentis martinae (Coen-Aubert, 1996)
Figure 7K–M

    1995b *Enallophrentis* n. sp.; Schöder, p. 380, pl. 1, figs 1, 2.
   *1996 *Breviphrentis martinae* n. sp.; Coen-Aubert, p. 24, pl. 1, figs 1–5, pl. 2, figs 1–3.
    1996 *Enallophrentis rhenana* n. sp.; Schröder *et al.*, pp. 18, 19, pl. 1, figs 1–3, pl. 2, figs 4–8, pl. 3, figs 9–14, pl. 4, figs 15–18.

Material. – Resteigne (RES I-2/2, RES I-3/1 éb., RES I-3/7 éb.).

Diagnosis. – See Coen-Aubert (1996).

Description. – Specimens with 36 to 54 septa of both orders at a diameter of 25 mm to 40 mm. The major septa almost reach the centre of the corallum but leave a free space. The major septa are commonly thickened and their axial ends are commonly curled (see also Coen-Aubert 1996, pl. 2, fig. 4) in a poorly defined axial structure. The minor septa are half as long as the major septa. The cardinal fossula is conspicuous in juvenile stages (Fig. 7M) but tends to be less deep in more advanced stages of growth (Fig. 7K, L). The bilateral symmetry is variably marked. The external wall is up to 2.2 mm-thick. In longitudinal section, the tabulae are complete or irregularly divided, commonly convex with the axial part domed and the lateral part forming a peripheral gutter.

Discussion. – Coen-Aubert (1996) described from Resteigne *Breviphrentis martinae*. However, Pedder (2002) and Wrzołek (2002) challenged the generic attribution regarding the lack of calicinal expansions and axially thickened bifurcated and twisted long major septa almost forming an axial structure with the domed tabulae. Together with the thick stereozone and bilateral symmetry materialised by the cardinal fossula and a trochoid habitus, these characters suggest a generic attribution to

Enallophrentis Oliver, 1993 rather than *Breviphrentis*. Almost simultaneously Schröder *et al.* (1996) introduced *Enallophrentis rhenana* based on material from the upper Eifelian Freilingen Fm. of the Eifel Mts which, compared to Coen-Aubert's species, is slightly larger (34–50 mm in diameter and 49–58 septa of both orders). However *E. martinae* (Coen-Aubert, 1996) topotypes show that the range of this species is wider than the original material and covers the same area of variation than *E. rhenana* (Schröder *et al.*, 1996), with the same thickened stereozone, long minor septa, twisted and thickened axial ends of the major septa and a cardinal fossula. Being moreover of the same age (*ensensis* conodont Zone), we consider *E. rhenana* and *E. martinae* to be synonymes. *E. martinae* being published earlier (June 1, 1996) than the German species (July 31, 1996), it has the priority. From the Polish early Givetian species *E. corniformis* (Gürich, 1896) that display similar size and number of septa (35–50 septa of both orders at 19–48 mm in diameter after Wrzołek 2002), it differs by longer minor septa and the limited development of thickening in early stages. The late Eifelian-early Givetian form ?*E.* sp. described by Schröder & Kazmierczak (1999) from the Ouihalane reef of Morocco differs by the dilatation of the septa limited in the cardinal quadrants.

Occurrence. – *Enallophrentis martinae* (Coen-Aubert, 1996) occurs in the late Eifelian (*ensensis* conodont Zone) Hanonet Fm. of S Belgium and Freilingen Fm. of the Eifel Mts (Schröder *et al.* 1996).

Family Phillipsastreidae Roemer, 1883

Genus *Macgeea* Webster, 1889

Type species. – *Pachyphyllum solitarium* Hall & Whitfield, 1873.

Diagnosis. – See Coen-Aubert & Wrzołek (1991).

Macgeea bathycalyx (Frech, 1886)
Figure 8H

e.p. *1886 *Cyathophyllum bathycalyx* n. sp.; Frech, pp. 181, 182, pl. 19, figs 8–11, (*non* pl. 17, figs 17–24).
    1996 *Macgeea bathycalyx bathycalyx* (Frech, 1886). – Schröder, p. 55, pl. 1, figs 1–8, pl. 2, figs 9–17. [*cum syn.*]

Material. – Resteigne (RES II-8/7) and Couvin (COUV I-2/1, COUV I-6/14).

Diagnosis. – See Birenheide (1978).

Description. – Specimens with 28 to 33 septa of both orders (30 on average) at a diameter of 13 mm to 19 mm
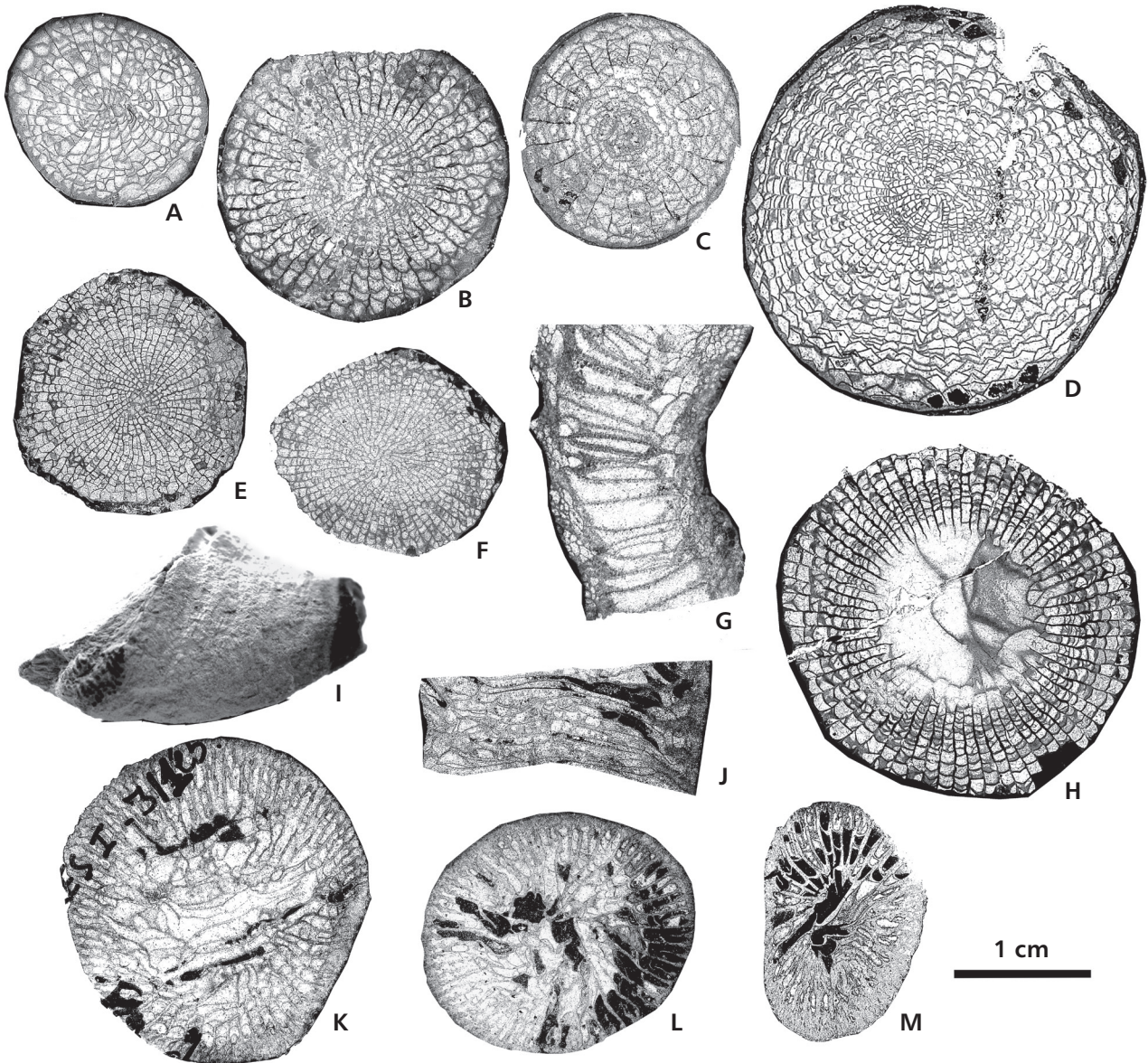
Figure 7. Ptenophyllid, dysphyllid, goniophyllid and zaphrentid rugose corals from the Hanonet Formation. • A–C – *Grypophyllum* cf. *denckmanni* Wedekind, 1922, specimen NIS-Est/4 from Nismes, TS (A), specimen COUV I-5/1 éb. from Couvin, TS (B) transverse section, specimen COUV I-6/11 from Couvin, TS (C). • D – *Grypophyllum* sp., specimen WLM/37b from Wellin, TS. • E, F – ?*Grypophyllum* sp., specimen COUV I-6/6 from Couvin, TS (E), specimen RES II-9/15 from Resteigne, TS (F). • G, H – *Aristophyllum luetti* Coen-Aubert, 1997, specimen JML-M/2 from Jemelle, TS (G), specimen RES I-9/6 from Resteigne, LS (H). • I – *Calceola sandalina* (Linnaeus, 1771), specimen from Resteigne disused Quarry, unit 5, lateral view. • J–M – *Enallophrentis martinae* (Coen-Aubert, 1996), specimen RES I-3/7 éb. from Resteigne, LS (J) and TS (K), specimen RES I-3/1 éb. from Resteigne TS (L) and specimen RES I-2/2, in a juvenile, from Resteigne TS (M). Magnification ×2 for all specimens.

(15 mm on average). The major septa are long but do not reach the axis of the corallum and leave a free space. Both orders of septa are thickened especially over the horseshoes dissepiments. The minor septa are half as long as the major septa and confined to the dissepimentarium. The dissepimentarium typically consists of 2 rows of thickened regular concentric dissepiments, the external row with the concavity oriented towards wall whereas the inner row has the concavity towards the axis, the opposite directions of concavity witness the intersection of the horseshoe dissepiments by the transverse section (Fig. 8H). The width of the tabularium varies from 9.8 mm to 12.8 mm. In longitudinal section, the dissepiments are horizontal near the wall and are inclined at an angle up to 45° in the inner rows. The tabulae are complete, subhorizontal and there are 14–16 tabulae/cm.

Discussion. – With an average diameter of 15 mm for 30 septa of both orders, this material is similar to the specimens attributed to *Macgeea bathycalyx* by Tsien (1969), Birenheide (1978) and Schröder (1995a, 1996). The colonial faciculate phillipsastreid *Thamnophyllum occlusum* (Tsien, 1969) occurring also in the same strata displays a very similar morphology but isolated corallites can be distinguished from small-sized sections of *M. bathycalyx* by a higher ratio of number of septa diameter.

Occurrence. – This species occurs at Couvin and Resteigne, in the entire Hanonet Fm., below and above the Eifelian–Givetian boundary. *Macgeea bathycalyx* is known from the upper Eifelian and lower Givetian of the Eifel Mountains (Junkerberg, Freilingen and Ahbach formations) (Birenheide 1978, Schröder 1996).

Family Ptenophyllidae Wedekind, 1923

Genus *Dohmophyllum* Wedekind, 1923

Type species. – *Dohmophyllum involutum* Wedekind, 1923.

Diagnosis. – See Pedder *in* Pedder *et al*. (1971).

Dohmophyllum aff. _difficile_ (Wedekind, 1925)
Figure 9D, E

> 1998 *Dohmophyllum* sp. cf. *difficile* (Wedekind, 1925). – Schröder, p. 55, pl. 12, figs 77, 78.

Material. – Couvin (COUV I-4/6, COUV I-6/5, COUV I-6/5, COUV I-7/4) and Nismes (NIS-Est/5, NIS-Est/8, NIS-Est/14, NIS-Ouest/4).

Description. – Specimens with 29 to 36 septa of both orders (31 on average) at a diameter of 17 mm to 42 mm (25–30 mm commonly). The major and the minor septa are of similar thickness and bear some carinae in the tabularium. The major septa reach usually the axis of the corallum where they are twisted to form a vortex (Fig. 9D, E). The minor septa are generally long (up to 90% of the length of the major septa). The dissepimentarium includes 13 to 22 rows (18 on average) of concentric or angulo-concentric interseptal dissepiments, the external row occasionnaly displaying flat dissepiments. The width of the narrow tabularium varies from 5.8 mm to 13.7 mm.

Discussion. – The specimens are slightly smaller (25–30 mm of diameter) than those identified by Birenheide (1963) (25–60 mm with a mean value of 40 mm), Birenheide (1978) (40–45 mm) and Schröder (1998) (45 mm). Nevertheless the number of septa of the analysed specimens (31 to 32 of both orders) is similar to the number observed by Birenheide (1978) (32 to 34 of both orders) and Schröder (1998) (30 to 40 of both orders). The tabularium width (5.8–13.7 mm) is similar to the one observed by Birenheide (1963) (~10 mm) and Schröder (1998) (5–14 mm). This species differs from *Dohmophyllum wedekindi* by the presence of a more or less pronounced vortex.

Occurrence. – This species was identified at Couvin and Nismes, in the middle and upper parts of the Hanonet Fm., in the *hemiansatus* Zone. *D. difficile* and similar species (*e.g. D.* cf. *difficile* in Schröder 1998) is known from the Eifelian and the Givetian of the Eifel Mountains (Nohn up to Dreimühlen formations) and Sauerland (Oberhonseler Fm.; Birenheide 1963, 1972, 1978; Schröder 1998).

Dohmophyllum wedekindi Birenheide, 1972
Figure 9B, C

> 1925 *Pseudoptenophyllum* sp. – Wedekind, pl. 16, figs 95, 96.
> *1972 *Dohmophyllum weidekindi* n. sp.; Birenheide, pp. 422–424, text-figs 9–13.
> 1978 *Dohmophyllum wedekindi* (Birenheide, 1972). – Birenheide, pp. 142, 146, text-fig. 89.

Material. – Couvin (COUV I-6/1).

Diagnosis. – See Birenheide (1978).

Description. – Specimens having 26 septa of both orders at a diameter of 33 mm. The minor and the major septa are of a similar thickness. The major septa reach the axis of the corallum where they are twisted and form a weak vortex. The minor septa are ¾ as long as the length of the major septa. The dissepimentarium includes 16 to 18 rows of dissepiments. The outer dissepimentarium comprises some narrow lonsdaleoid and regular concentric interseptal dissepiments whereas the inner dissepimentarium comprises angulo-concentric, herringbone and arched dissepiments (Fig. 9B). The tabularium is narrow (8.8 mm in diameter).

Discussion. – This specimen is similar (26 septa of both orders at a diameter of 33 mm) to the ones discribed by Birenheide (1972) (27 septa of both orders at a diameter of 25 mm) and Birenheide (1978) (26 to 28 septa of both orders at a diameter varying from 25 mm to 35 mm). This species differs from *Dohmophyllum* aff. *difficile* by the weakly pronounced vortex and the more complex composition of the dissepimentarium that includes lonsdaleoid dissepiments.

Distribution. – The specimen is from the upper part of the Hanonet Fm. (*hemiansatus* Zone) in the Couvin section.
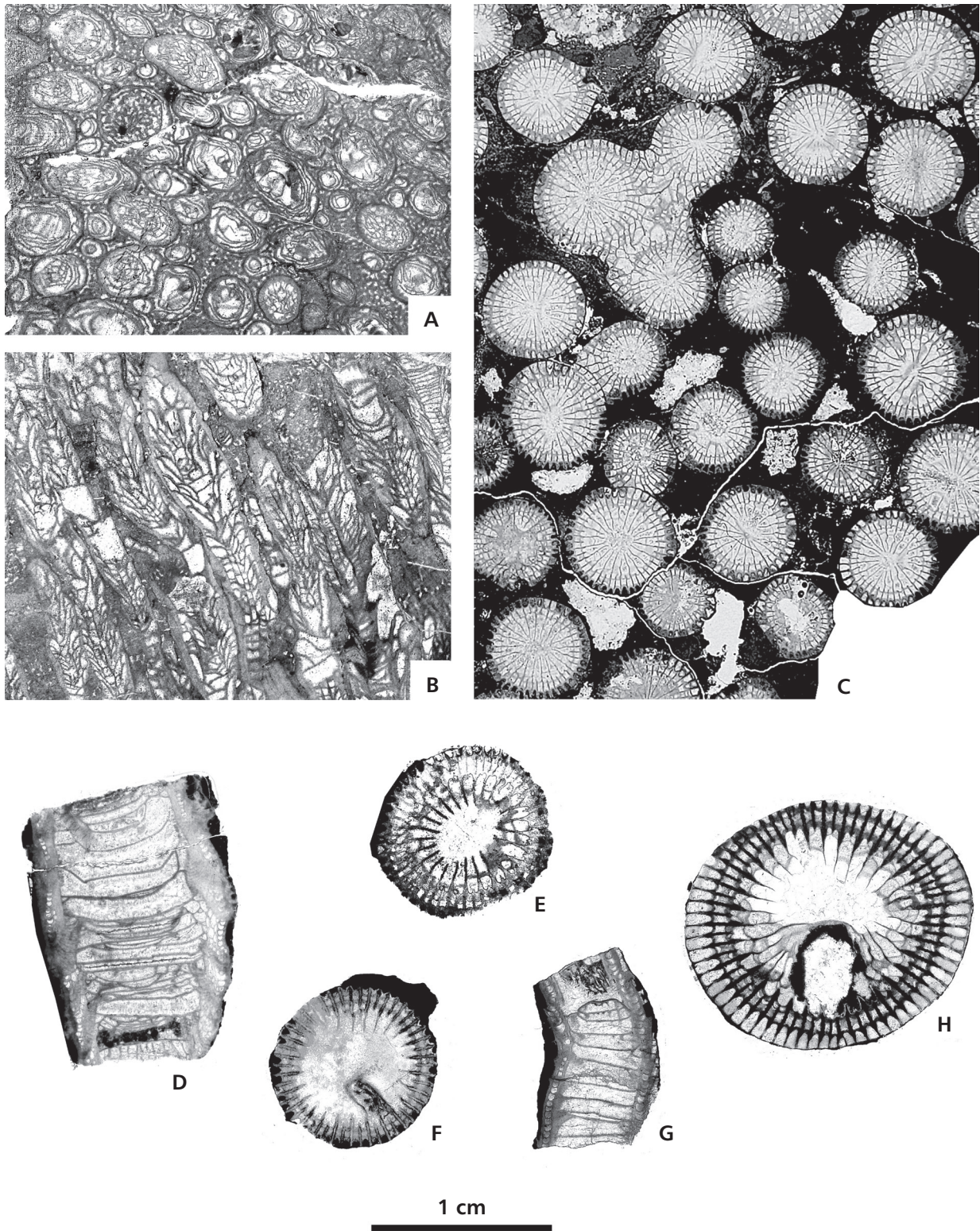
Figure 8. Ptenophyllid and philipsastreid rugose corals from the Hanonet Formation. • A, B – *Neomphyma dalcqae* Coen-Aubert, 1992, specimen BZ-1 from Baileux zoning, TS (A) and LS (B). • C–G – *Thamnophyllum occlusum* (Tsien, 1969), specimen Couvin 10 from Couvin, TS (C), specimen COUV I-5/5 from Couvin, LS (D) and TS (E), specimen RES II-9/1 from Resteigne, TS (F), specimen COUV I-6/8 from Couvin, TS (G). • H – *Macgeea bathycalyx* (Frech, 1886), specimen COUV I-2/1 from Couvin, TS. Magnification ×3 for all specimens.

Birenheide (1972, 1978) identified this species in the Givetian (Loogh Fm.) of the Eifel Mountains (W Germany).

Family Stringophyllidae Wedekind, 1925

Genus *Stringophyllum* Wedekind, 1922

Type species. – *Stringophyllum normale* Wedekind, 1922.

Diagnosis. – See Coen-Aubert (2011).

Stringophyllum acanthicum (Frech, 1885)
Figure 10A, B

> *1885   *Endophyllum acanthicum* nov. sp.; Frech, p. 929, pl. 41, fig. 5.
> 2011   *Stringophyllum acanthicum* (Frech, 1885). – Coen-Aubert, p. 31, pl. 1, figs 1–6, pl. 2, figs 8, 9, pl. 3, fig. 4. [*cum syn.*]

Material. – Nismes (NIS-Est/3, NIS-Est/13).

Diagnosis. – See Coen-Aubert (2011).

Description. – Specimens with 46 to 48 septa of both orders at a diameter of 27 to 31 mm. The septa are commonly dilated in the tabularium. The major septa almost reach the axis of the corallum where they usually join in irregular bundles, highlighting the bilateral symmetry (Fig. 10A, B). The minor septa are $^2/_3$ to $^4/_5$ as long as the length of the major septa and are confined to the dissepimentarium where they are commonly discontinuous with isolated septal crest on the dissepiments. The wall is thickened. The dissepimentarium comprises 6–7 rows of interseptal, regular concentric and oblique dissepiments, the outer row being made of large flat lonsdaleoid dissepiments. The width of the tabularium varies from 8.3 to 9.3 mm.

Discussion. – The present specimens have a size and a number of septa very similar to those of specimens attributed to *S. acanthicum* by Kettnerová (1932), LeMaître (1947), Tsien (1969), Birenheide (1978), Schröder (1995a, b, 1997c, 1998) and Coen-Aubert (2011). This species differs from *Stringophyllum buechelense* by the presence of strongly thickened major septa and the larger size of the corallum (30 mm for the present species versus 20 mm for *S. buechelense*).

Occurrence. – The two specimens come from the disused Nismes quarry exposing the Givetian part of the Hanonet Fm. This species is known from the upper Eifelian and the lower Givetian (Ouihalane "coral reef") of Moroccan Ma'der Basin (LeMaître 1947, Coen-Aubert 2011), in the

upper Eifelian and the Givetian of the Eifel Mountains, in the Nims Mb. (upper part of the Jurkerberg Fm.), the Freilingen Fm., the Cürten Fm. and the Rodert Fm., Sauerland (W Germany) in the Schwelm Fm., Belgium (uppermost part of the Jemelle Fm. up to the lower part of the Trois-Fontaines Fm., Coen-Aubert 2011), England and France (Chalonnes Fm. of Brittany, Coen-Aubert 2011) (Birenheide 1978; Schröder 1995a, 1997c, 1998), in the Givetian of Moravia (Czech Republic, Kettnerová 1932) and possibly also in Russia (Urals, Shurigina 1972).

Stringophyllum buechelense (Schlüter, 1889)
Figure 10C–G

> *1889   *Spongophyllum buechelense* Schlüter; Schlüter, p. 63, pl. 7, fig. 8.
> 2005   *Stringophyllum buechelense* (Schlüter, 1889). – Schröder, p. 102, pl. 10, figs 9–12. [*cum syn.*]

Material. – Resteigne (RES indét., RES I-8/2 éb.+ pl. d, RES II-9/10, RES II-9/16 a–b et c, RES II-9/19), Couvin (COUV I-6/13, COUV I-7/1) and Nismes (NIS-Est/16).

Diagnosis. – See Birenheide (1978).

Description. – Specimens with 32 to 40 septa of both orders at a diameter of 19 mm to 24 mm. The septa are slightly dilated. The major septa almost reach the axis of the corallum where they are usually joined in irregular bundles, highlighting the bilateral symmetry (Fig. 10D). The minor septa are $^2/_3$ as long as the length of the major septa and are confined to the dissepimentarium where they are commonly discontinuous. The wall is thickened. The dissepimentarium comprises 4 to 13 rows (commonly 6 to 9) of transeptal, regular and herringbone dissepiments, the outer row comprising large and flat lonsdaleoid dissepiments. The width of the tabularium varies from 4.1 mm to 8.7 mm. In longitudinal section, the dissepiments are inclined at an angle of 45–50° towards the tabularium (Fig. 10C, F). The tabulae are almost complete and slightly depressed axially. There are 18–27 tabulae/cm.

Discussion. – As the present specimens have a size and a number of septa very similar to those of *S. buechelense*, *e.g.* in LeMaître (1947), Tsien (1969), Schröder (1995a, 2005) and Schröder & Kazmierczak (1999), they are confidently attributed to this species. However, the specimens figured by Birenheide (1978) and May (1993) display a larger tabularium (1/2 of the corallum diameter) despite a similar number of septa.

Distribution. – This species is present in Couvin, Nismes and Resteigne, in the middle and upper parts of the Hanonet Fm., above the Eifelian–Givetian boundary. The species is
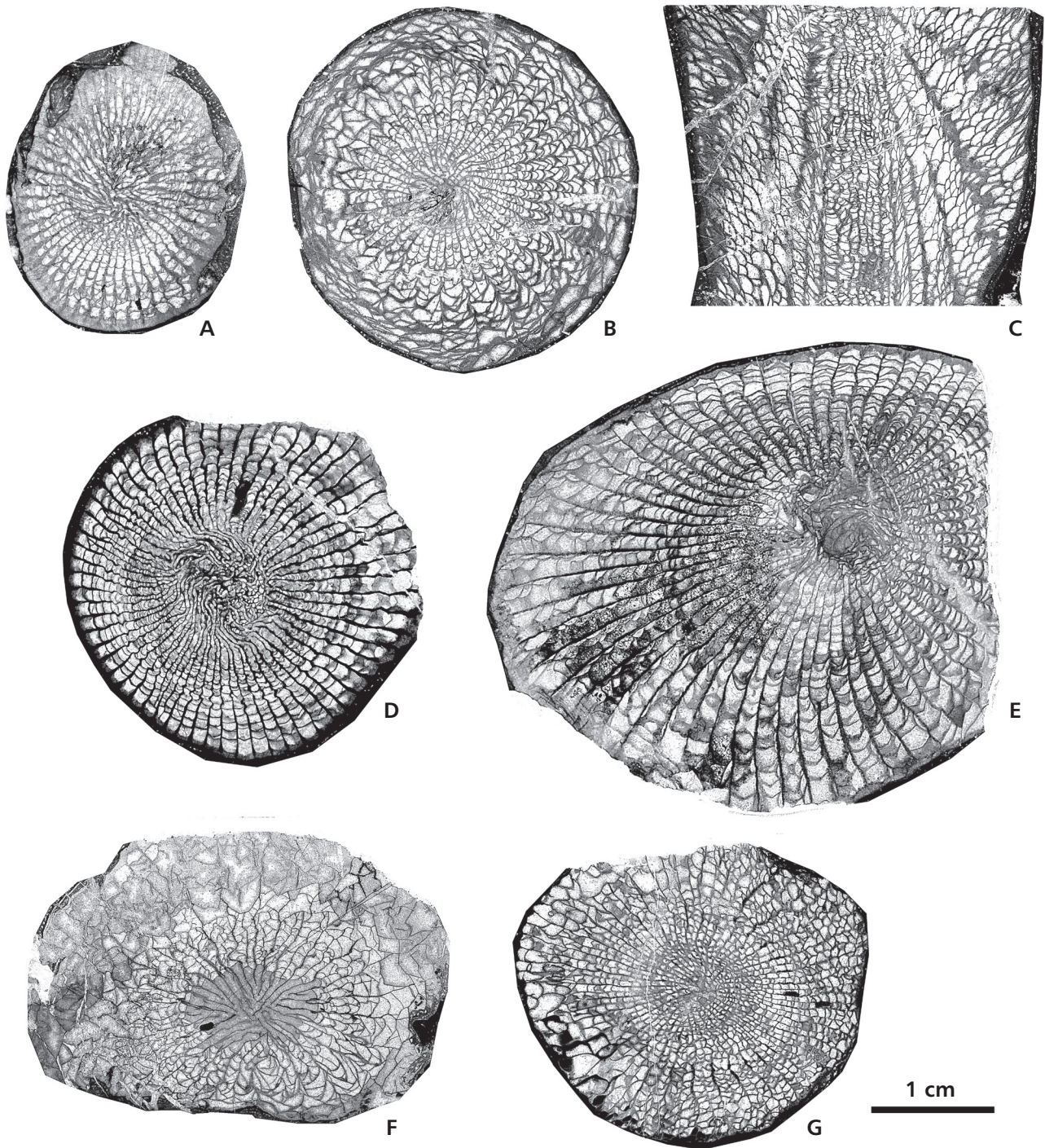
Figure 9. Ptenophyllid rugose corals from the Hanonet Formation. • A – *Acanthophyllum* sp. 2, specimen NIS-Est/12 from Nismes, TS. • B, C – *Dohmophyllum wedekindi* Birenheide, 1972, specimen COUV I-6/1 from Couvin, TS (B) and LS (C). • D, E – *Dohmophyllum* aff. *difficile* (Wedekind, 1925), specimen NIS-Est/8 from Nismes, TS (D), specimen NIS-Est/5 from Nismes, TS (E). • F, G – *Dohmophyllum* sp., specimen NIS-Est/17 from Nismes, TS (F) transverse section, specimen COUV I-4/3 from Couvin, TS (G). Magnification ×2 for all specimens.

known from the Eifelian and Givetian of W Germany in the Sauerland (Bredenburch Mb. of the Unterhonsel Fm. and in the Oberhonseler Fm.) and in the Eifel Mountains (Cürten and Kerpen formations) and also in France,

Poland, England (Joseph & Tsien 1975; Birenheide 1978; May 1993; Schröder 1995a, 2005). This species is also known from the lower Givetian of the eastern Anti-Atlas (Ouihalane "coral reef") in Morocco (LeMaître 1947,

Schröder & Kazmierczak 1999) and in the lower Givetian strata of E Australia (described as *S. irregulare* Hill, 1942).

Family Pycnostylidae Stumm *in* Shrock & Twenhofel (1953)

Genus *Cyathopaedium* Schlüter, 1889

Type species. – *Calophyllum paucitabulatum* Schlüter, 1880.

Diagnosis. – See Hill (1981).

Cyathopaedium paucitabulatum (Schlüter, 1880)
Figure 11L–N

> *1880 *Calophyllum paucitabulatum* sp. n.; Schlüter, p. 52.
> ? 1885 *Amplexus multiseptatus* n.; Maurer, p. 84, pl. 1, figs 11–18.
>   1894 *Coelophyllum paucitabulatum* Schlüter. – Weissermel, p. 636, text-fig 1.
>   1883 *Calophyllum radicans* n. Schulz; Schulz, p. 74, pl. 21, figs 1–4.
>   1969 *Amplexus champernownei* Smith & Thomas, 1963. – Tsien, p. 145, pl. 22, figs 1, 2.
>   1978 *Cyathopaedium paucitabulatum* (Schlüter, 1880). – Birenheide, pp. 186, 187, pl. 21, fig. 2.
>   2002 *Cyathopaedium* sp. – Schröder, pp. 178, 180, pl. 1, figs 1–9, pl. 2, fig. 11.

Material. – Resteigne (RES I-6/1, RES II-5/1, RES II-5/4, RES II-5/5, RES II-5/6 a–e, RES II-5/17).

Diagnosis. – See Birenheide (1978).

Description. – Specimens with a diameter of 11 mm to 22 mm. There are <60 very rudimentary septa (Fig. 11M), where developed and thickened in continuity with the wall, stereoplasma commonly filling the interseptal loculi. The thickness of the wall varies from 0.5 to 2.2 mm. The wall is festooned internally (Fig. 11L). The tabulae are subhorizontal or infundibuliform, vesicular and irregularly space (2–5 mm between individual tabula) (Fig. 11N).

Discussion. – The genus *Cyathopaedium* – together with *Stylopleura*, *Fletcheria*, *Maikottia* and *Pycnostylus* are based on morphologically simple species displaying calinical buddings, short undifferenciated septa confined to the wall, widely-spaced tabullae and no dissepimentarium (Pedder 1976, Schröder 2007). Their very simple morphology makes them similar and without a revision of these forms (including habitus), synonymy can not be discarded. However, with its long cylindrical corallites, the present specimens ressemble material attributed to *Cyathopaedium* Schlüter, 1880 which differs from *Stylopleura* Merriam, 1974b by its habitus (the American genus displaying ceratoid or subcylindrical corallites). Birenheide (1978) recognized two different species in the genus *Cyathopaedium*: *C. paucitabulatum* (Schlüter, 1880) with 48 septa at a diameter of 25 to 40 mm and tabulae spaced 25–30 mm apart, and *C. radicans* (Schulz, 1883) with 60 septa at a diameter of 30 to 50 mm and tabulae spaced by *c*. 1 cm. However, in the present material, there is a continuum variation from small individuals to large ones, with no discrete boundary or differences in characters. Keeping in mind that these corals are very simple and morphologically malleable, it would seem suitable to group all individuals in a single species under the name *C. paucitabulatum* Schlüter, 1880. Schröder (2002) suggested that several species described under the generic name *Amplexus* in the Devonian of Germany might also be representants of *Cyathopaedium* but without a carefull revision, notably of the ontogeny of the material, their synonymy remains hypothetical.

Occurrence. – This species is present at Resteigne, in the lower and middle parts of the Hanonet Fm., below and above the Eifelian–Givetian boundary. The species *C. paucitabulatum* is known from the Givetian of W Germany (Büchel Fm.) whereas the species *C. radicans* is known from the Givetian of the Eifel Mountains (from Loogh to Dreimühlen formations) (Birenheide 1978).

Family Tryplasmatidae Etheridge, 1907

Genus *Tryplasma* Lonsdale, 1845

Type species. – *Tryplasma aequabile* Lonsdale, 1845.

Diagnosis. – See Glinski (2001).

Tryplasma rohrense Glinski, 2001
Figure 11I–K

> * 2001 *Tryplasma rohrensis* n. sp.; Glinski, p. 74, figs 1–14, 16.

Figure 10. Stringophyllid rugose corals from the Hanonet Formation. • A, B – *Stringophyllum acanthicum* (Frech, 1885), specimen NIS-Est/3 from Nismes, TS (A), specimen NIS-Est/13 from Nismes, TS (B). • C–G – *Stringophyllum buechelense* (Schlüter, 1889), specimen RES II-9/16 from Resteigne, TS (C) and LS (D), specimen NIS-Est/16 from Nismes, TS (E) and LS (F), specimen RES II-9/10 from Resteigne, TS (G). • H – *Sociophyllum torosum* (Schlüter, 1881), specimen Couvin 22e from Couvin, TS. Magnification ×2 for all specimens.
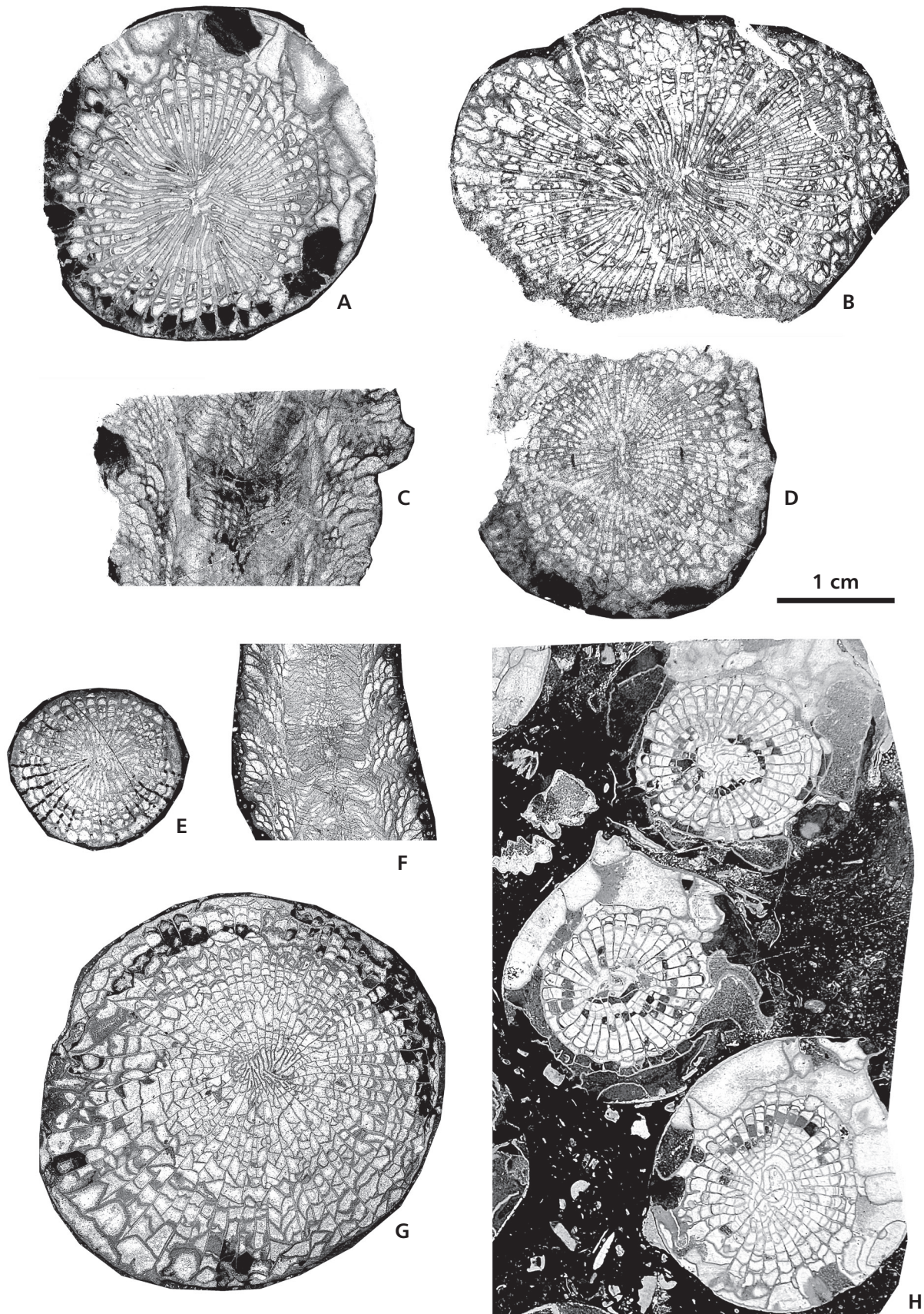
Material. – Resteigne (RES II-5/6 f–h), Baileux (BAI-1) and Couvin (Couvin/17).

Diagnosis. – See Glinski (2001).

Description. – Specimens with 36 to 38 septa of both orders at a diameter of 15 mm to 29 mm. The septa are very short (up to 3.3 mm at a diameter of 28 mm, Fig. 11I). The minor septa are ¾ to ⁴⁄₅ as long as the length of the major septa. The septa are rudimentary and thickened in continuity with the wall, particularly in juvenile stages (Fig. 11J), when the spaces between the septa are entirerly filled with stereoplasma. The wall varies from 0.7 to 2 mm-thick. The tabulae are subhorizontal or slightly infundibuliform, vesicular and irregularly-space (2–5 mm between individual tabula).

Discussion. – The studied specimens fit in the description made by Glinski (2001) for *Tryplasma rohrense* except that the present specimens are slightly larger (up to 29 mm in diameter). They differ from fragments of *Cyathopaedium paucitabulatum* (Schlüter, 1880) occurring in the same beds by the septal development.

Occurrence. – This species is present in Couvin, Baileux and Resteigne, in the lower and middle parts of the Hanonet Fm., below and above the Eifelian–Givetian boundary. This species is known from the Eifelian of the Eifel Mountains (Arhdorf Fm.) (Glinski 2001).

Order Cystiphyllida Nicholson *in* Nicholson & Lydekker, 1889

Family Cystiphyllidae Milne-Edwards & Haime, 1850

Genus *Cystiphylloides* Chapman, 1893

Type species. – *Cystiphyllum aggregatum* Billings, 1859.

Diagnosis. – See McLean (1976).

***Cystiphylloides macrocystis* (Schlüter, 1889)**
Figure 11A–D

*1889   *Cystiphyllum macrocystis* Schlüter; Schlüter, p. 88, pl. 3, fig. 10.

1995a   *Mesophyllum* (*Cystiphylloides*) *macrocystis macrocystis* (Schlüter, 1889). – Schröder, p. 53, pl. 8, fig. 41, text-fig. 11. [*cum syn.*]

1998   *Mesophyllum* (*Cystiphylloides*) *macrocystis macrocystis* (Schlüter, 1889). – Schröder, pp. 75, 76, pl. 21, fig. 123, pl. 23, fig. 128.

1999   *Mesophyllum* (*Cystiphylloides*) *macrocystis macrocystis* (Schlüter, 1889). – Schröder & Kazmierczak, p. 104, pl. 3, fig. 23.

Material. – Resteigne (RES I-2/1, RES I-3/2 éb., RES I-3/6 éb., RES I-9/2, RES II-5/12, RES II-5/14, RES II-5/14, RES II-5/2 éb., RES II-5/7 éb., RES II-7/1 éb., RES II-9/4), Couvin (COUV I-2/2-3, COUV I-6/10), Nismes (NIS-Ouest/6) and Jemelle (JML-M/5).

Diagnosis. – See McLean (1976).

Description. – Specimens 15 mm to 41 mm in diameter. The outer zone comprises medium-sized (1 mm on average) dissepiments near the wall and large-sized (1.5 to 2 mm) dissepiments/tabellae near the axis of the corallum (Fig. 11E). The dissepiments are globose at the periphery and tend to be elongated near the axis (Fig. 11A). Many corallites display an eccentric axis. There are narrow septal crusts resting on the thickened wall. Thick layers of stereoplasma occur in the middle part of the outer zone. In longitudinal section, the dissepiments are inclined at an angle of 55 to 70° and forming a sagging layer (Fig. 11B).

Discussion. – The morphological caracteristics of *C. macrocystis* are well shown in the present specimens. They display the same range of variability as the specimens attributed to that species and figured by Tsien (1969), McLean (1976), Birenheide (1964, 1978), Pedder & McLean (1982), Soto & Lin (1995), Schröder (1995a, 1998) and Schröder & Kazmierczak (1999). This species differs from the other species of *Cystiphylloides* by the presence of the eccentric axis combined with the well developed septal crust, with the presence of smaller dissepiments at the periphery and larger dissepiments/tabellae near the axis and with

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Figure 11. Cystiphyllid tryplasmatid and pycnostillid rugoe corals from the Hanonet Formation. • A–D – *Cystiphylloides macrocystis* (Schlüter, 1889), specimen RES II-5/7 éb. from Resteigne, TS (A) transverse section, specimen RES II-9/4 from Resteigne, LS (B), specimen RES I-2/1 from Resteigne, TS (C), specimen COUV I-2/2 from Couvin, TS (D). • E, F – *Cystiphylloides* sp., specimen RES II-5/18 from Resteigne, TS (E), specimen RES I-6/1 éb. from Resteigne, TS (F). • G, H – *Microplasma* sp., specimen RES I-7/3 from Resteigne, LS (G) and TS (H). • I–K – *Tryplasma rohrense* Glinski, 2001, specimen BAI-1 from Baileux quarry, TS (I) transverse section, specimen Couvin/17 from Couvin, TS (J) in a juvenile stage, stereoplasma feeling the space between the septa and hiding them and TS (K) in a mature stage, septa going through the stereoplasma. • L–N – *Cyathopaedium paucitabulatum* (Schlüter, 1880), specimen RES I-6/1 from Resteigne, TS (L), view of the festooned morphology, specimen RES II-5/5 from Resteigne, TS (M), specimen RES I-5/6 from Resteigne, LS (N). Magnification ×2 for A–I and M,N; and ×12 for J,K; and ×20 for L.
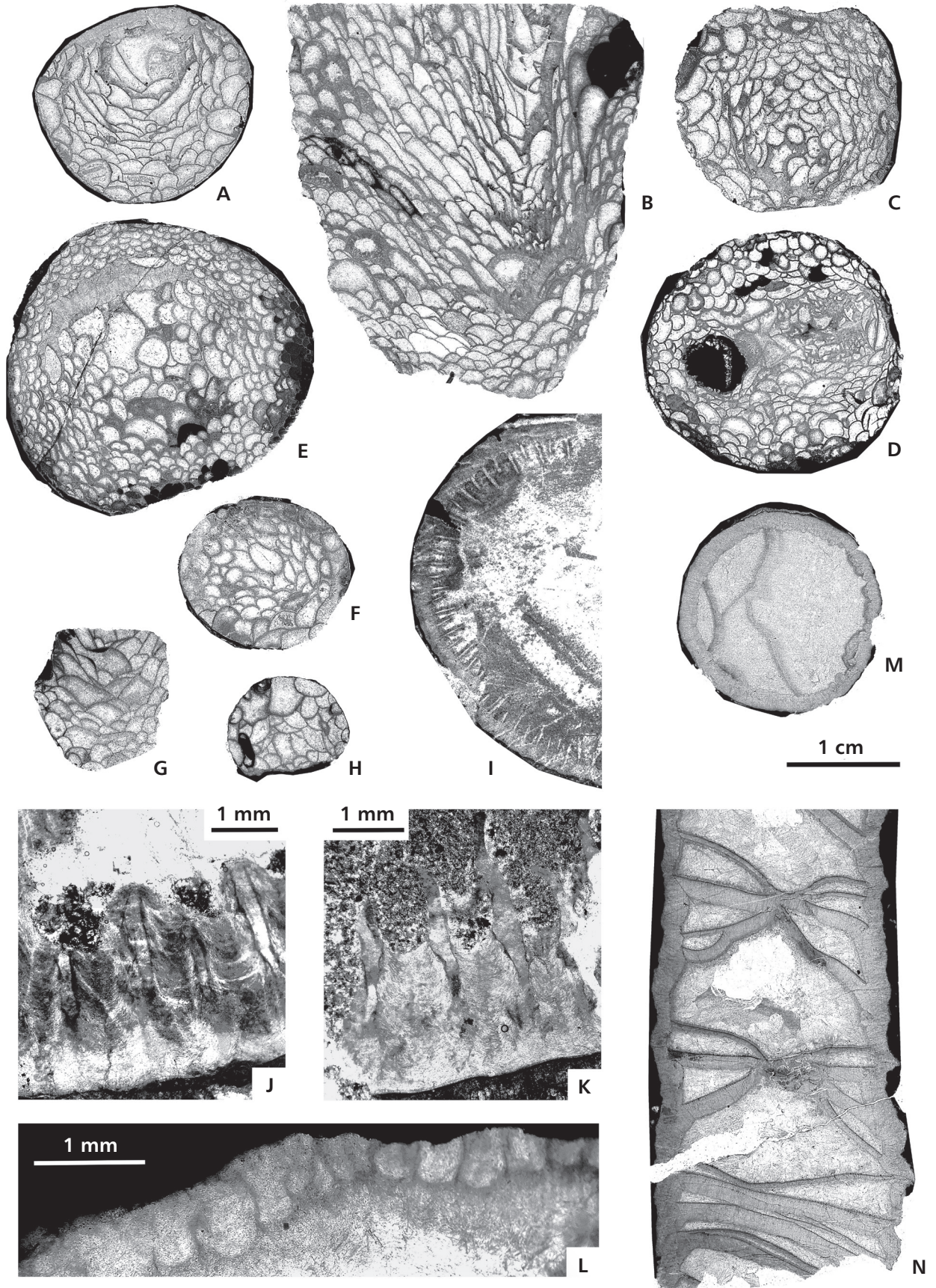
the steeply inclined dissepiments forming a sagging layer.

Occurrence. – The species is a common component of the coral fauna in the Hanonet Fm., in the localities Couvin, Jemelle, Nismes and Resteigne, both in the upper Eifelian *ensensis* Zone and in the lower Givetian *hemiansatus* Zone. This species, is also a common component of the Lower–Middle Devonian fauna, known from the Pragian of Tasmania (Pedder & McLean 1982; Schröder 1995a, 1998), from the Emsian of the Kuznetsk Basin (Bulvanker 1958), from the uppermost Emsian Shanda beds of the Altay Mountains (Pedder & McLean 1982), from the Eifelian of the Gansu Province (Central China, Soto & Lin 1995), from the upper Eifelian Hume Fm. of Canada (Mackenzie District) (Pedder & McLean 1982), from the Eifelian and Givetian of the Eifel Mountains (Jurkerberg to Dreimülhen formations, Birenheide 1964, 1978), Belgium (Tsien 1969), from the lower Givetian of Afghanistan (Pedder & McLean 1982), eastern Anti-Atlas (Ouihalane "coral reef") in Morocco (Schröder 1995a, 1998; Schröder & Kazmierczak 1999), Transcaucasus (Ulitina 1968), Kuznetsk Basin (Padiskyii horizon, Bulvanker 1958) and northern Urals (Soshkina 1936).

Family Digonophyllidae Wedekind, 1923

Genus *Mesophyllum* Schlüter, 1889

Type species. – *Actinocystis defecta* Schlüter, 1882.

Diagnosis. – See Hill (1981).

***Mesophyllum vesiculosum* (Goldfuss, 1826)**
Figure 12A

   *1826   *Cyathophyllum vesiculosum* nobis; Goldfuss, p. 58, pl. 17, fig. 5e.
   1993   *Mesophyllum* (*Mesophyllum*) *vesiculosum vesiculosum* (Goldfuss 1826). – May, pp. 60–62, pl. 10, fig. 4, text-fig. 15. [*cum syn.*]
   1998   *Mesophyllum* (*Mesophyllum*) *vesiculosum vesiculosum* (Goldfuss 1826). – Schröder, pp. 68, 69, pl. 18, figs 107, 108.
   1998   *Mesophyllum* (*Mesophyllum*) sp. cf. *vesiculosum vesiculosum* (Goldfuss 1826). – Schröder, p. 69, pl. 19, fig. 109.

Material. – Resteigne (RES I-8/1 éb.).

Diagnosis. – See Birenheide (1978).

Description. – Specimens with 41 septa of both orders at a diameter of 35 mm. The septa are discontinuous and reduced to trabeculae in the outer dissepimentarium (Fig. 12A). The major septa reach the centre of the corallum where they form a poorly-defined vortex. The major septa are slightly thicker than the minor septa. The minor septa are ¾ as long as the length of the major septa. The wall is thickened. The outer dissepimentarium consists of dissepiments of different size and shape. The inner dissepimentarium consists of regular dissepiments. The tabularium is 12.1 mm-wide. In longitudinal section, the dissepiments are inclined at an angle of 15–20° at the periphery, but as high as 55–60° near the axis.

Discussion. – The specimen displays the same morphological characters and size as those figured by LeMaître (1947), Birenheide (1964, 1978), May (1993) and Schröder (1998). The species is often referred to be colonial (*e.g.* Birenheide 1978) but clear offsets have rarely been reported (Birenheide 1964, May 1993, Schröder 1998), suggesting rather a gregarious habit. The present material being fragmented, it was not possible to determinate the habitus.

Occurrence. – The specimen is from Resteigne, from the middle part of the Hanonet Fm., above the Eifelian–Givetian boundary. This species is known in Germany from the late Eifelian to middle Givetian of the Eifel Mountains (Junkerberg to Kerpen formations) and in the early Givetian of W Sauerland (Birenheide 1964, 1978; May 1993; Schröder 1998). It is known in the Givetian of the French Pyrenees (Joseph & Tsien 1975) and in the Italian Carnic Alps (Charlesworth 1914). *Mesophyllum vesiculosum* is also known from the Eifelian and Givetian of North America and the lower Givetian of Morocco (LeMaître, 1947).

General discussions

On the Belgian shelf, the '*otomari* phase' of the Kačák event is seemingly hidden by Struve's Great Gap – corresponding to silicoclastic deposits, as in W Germany (see

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Figure 12. Digonophyllid rugose corals from the Hanonet Formation. • A – *Mesophyllum vesiculosum* (Goldfuss, 1826), specimen RES I-8/1 éb. from Resteigne, TS. • B–G – *Mesophyllum* sp.1, specimen RES II-5/2 from Resteigne, LS (B), specimen RES I-3/6 éb. from Resteigne, TS (C) in a juvenile and TS (D) in an adult, specimen COUV I-5/3 from Couvin, TS (E), specimen 2004/1d from Resteigne, LS (F), specimen 2004/1a from Resteigne, TS (G). • H–J – *Mesophyllum* sp. 2, specimen RES II-9/9b from Resteigne, TS (H) in a juvenile stage, specimen 2015.10.13/10a from Couvin, TS (I) in a mature stage, specimen RES II-9/9a from Resteigne, LS (J). Magnification ×2 for specimens A–E and ×1 for specimens F–J.

A–E = 1 cm

F–J = 1 cm
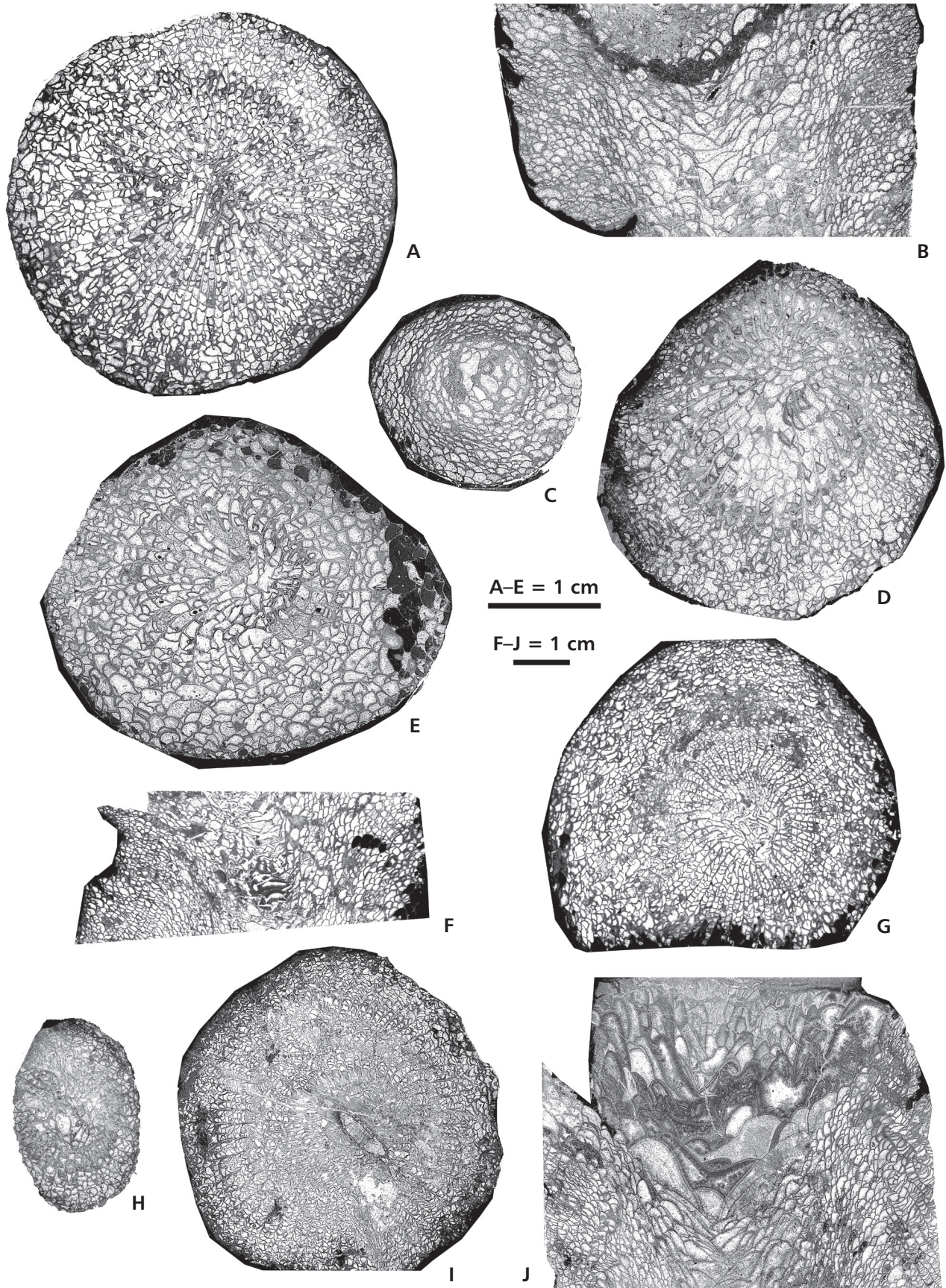
Struve 1982) – which left no trace of a biologic crisis (Bultynck & Hollevoet 1999). The second phase of the event was driven by a transgressive pulse that led to the deposition of argilo-carbonaceous deposits (Hanonet Fm. in Belgium and Freilingen Fm. in W Germany) (Bultynck & Hollevoet 1999, Königshof *et al.* 2016).

The lithological succession observed throughout the Hanonet Fm. is characterized by relatively dark argillaceous fine-grained limestone. As explained above, although they commonly display dark colour, there is no evidence of anoxia. The sediment is usually bioturbated and rather rich in benthic organisms (brachiopods, corals, gastropods, trilobites) and no organism is typical of oxygen-limited environment (paper-pecten, myodocopid ostracods, Casier *et al.* 1992). Again, there is no evidence that the Kačák event had a deleterious effect on the benthic fauna on the Belgian shelf.

This absence is the main difference with the German (House 1996, Walliser 1996, Schöne 1997), Czech (Chlupáč & Kukal 1988, House 1996) and others localities in bathyal settings where the Kačák event shows its most typical features. In shallow-water environments, the typical markers of the Kačák event (dacryoconarids, conodonts and ammonoids) are lacking and the identification of this biocrisis therefore has to be done with others proxies such as trace elements (Königshof *et al.* 2016) or biotic changes. Such biotic clues are here highlighted.

The lower third of the Hanonet Fm. yielded several coral species belonging to genera typical of the EAR that were unknown before the Hanonet Fm. and limited stratigraphically to this unit. These are *Enallophrentis martinae* (Coen-Aubert, 1996) and *Heliophyllum halleri* Schröder, 1995. The Siphonophrentidae genera *Breviphrentis, Enallophrentis* and *Siphonophrentis* (see Oliver 1993 for review) most probably originated in the EAR in the Early Devonian and became endemic and diverse in this realm during the Middle Devonian (Schröder 1997b, 2001; Oliver & Sorauf 2002). Pedder *in* Pedder & Feist (1998) has described two older (Emsian) species of *Breviphrentis* (*B. exigua* and *B. roharti*) from the Montagne Noire (France) which has some affinities with the northern margin of Gondwana. Scattered occurrences are known outside EAR: the late Eifelian *Enalloprentis martinae* (Coen-Aubert, 1996) (= *E. rhenana* Schröder *et al.*, 1996) in the Freilingen Fm. NE Eifel (Schröder *et al.* 1996) and Hanonet Fm. of Belgium (Coen-Aubert 1996), the late Eifelian–early Givetian ?*Enallophrentis* sp. from the Ouihalane reef of Morocco (Schröder & Kazmierczak 1999) and possibly the late Eifelian *Breviphrentis joae* Galle, 1995 from Moravia (Galle 1995) but its generic affinity was questioned by Schröder (2001) despite Oliver (1998)'s suggestion of considering it a synonyme of *B. simplex* Hall, 1843. Occurences in the Givetian in Eifel, Harz, Pyrenees, Devon, Holy Cross Mountains

are summarized in Schröder (2001) and Wrzołek (2002). Similarly *Heliophyllum* is a relatively common genus in the Lower and Middle Devonian strata of the EAR (Oliver & Sorauf 1988, Oliver 1997) that sporadically appears in the Middle Devonian strata of the OWR, in Western Europe in particular (Schröder 1997b). Schröder (1995a, b) reported *Heliophyllum halleri* n. sp. in the upper Eifelian Freilingen Fm. and Birenheide (1962) reported *Heliophyllum dahlmense* (Haller, 1936), Birenheide & Gabrielli (1993) precise it location in the lower Eifelian Nohn Fm., both in the Eifel Mountains. Additional upper Eifelian occurrences are from Moravia (Galle 1993), Transcaucasus and Urals (Dubatolov & Spasskiy 1964) and possibly from the Guangxi Province in South China (Oliver & Sorauf 1988). However, most *Heliophyllum* species are known from Givetian strata of the OWR (see Oliver & Sorauf 1988 and references therein). Their peculiar abundance in Spain and Morocco has to be noted (Oliver 1975). The genus *Moravophyllum* described as closely related to *Heliophyllum* by Birenheide (1987) and as a subgenus of *Heliophyllum* by Schröder (1995a, b) is present in the upper Eifelian Freiligen Fm. of the Eifel Mountains. LeMaître (1947) descried in the upper Eifelian–lower Givetian Ouihalane reef of Morocco some corals typical of the EAR including some heliophillids, siphonophrentids and *Eridophyllum seriale* Milne-Edwars & Haime, 1850 as the single occurrence of eridophyllid corals known outside North America.

In Spain and Morocco (Oliver 1975, Schröder & Kazmierczak 1999), the siphonophrentids and heliophyllids seem to be more abundant than in the rest of the OWR, possibly because of geographical proximity with the EAR as suggested by Schröder (2001).

Although limited, the occurrence of siphonophrentids and heliophyllids in the upper Eifelian strata of Western Europe seemingly coincides with the rapid eustatic rise associated with the Kačák event. The higher sea level at this period would have allowed the invasion of the EAR by OWR genera and would also have allowed the escape of EAR genera to the OWR as already suggested by Oliver (1973, 1975, 1976). So far, this sudden and short-term 'invasion' of EAR fauna on to the Belgian and western German shelves is the most reliable indication of where to place the main phase of the Kačák event.

Conclusions

Based on faunal changes in pelagic ecosystems, the Kačák event has been identified in many localities around the world (House 1996, 2002; Walliser 1996; DeSantis 2010). The lithological markers of the event typically correspond to the onset of anoxic black shales or dark dysoxic limestone. Typical markers are the joint appearances of the

dacryoconarid *Nowakia otomari*, the conodont *Polygnathus ensensis*, the ammonoids *Maenioceras* and *Agoniatites* and the diversification of *Cabrieroceras crispiforme*, *Holzapfeloceras* and *Wedkindella*, together with the disappearance of the dacryoconarid *Nowakia chlupaciana* and the conodont *Tortodus kockelianus* (Chlupáč & Kukal 1988, House 1996, Walliser 1996, Schöne 1997, Chlupáč *et al.* 2000, DeSantis 2010, Ellwood *et al.* 2011).

On a global scale, during this 200 ka-long interval (Ellwood *et al.* 2011, Kido & Suttner 2011), two of the three faunal realms that were present from the Emsian were dismantled (May 1995, Walliser 1996, DeSantis 2010). The Malvinokaffric Realm disappeared because of global increase of temperatures (May 1995, 1997a, 1997b; Walliser 1996; Boucot *et al.* 1997; Horodyski *et al.* 2014). A major transgressive pulse led to the breaching of a continental arch that separated the East Americas Realm from the Old World Realm. Consecutive invasions of fauna from OWR have seemingly driven the EAR fauna to extinction (Oliver 1990, May 1995, DeSantis 2010).

In Belgium, the lack of typical markers of the Kačák event made its identification more complicated. The abrupt arrival of heliophyllid and siphonophrentids rugose corals (extremely rare in Europe before and after the event, Oliver & Sorauf 1988, Schröder 2001) is likely linked to the late Eifelian transgression that triggered the Kačák event.

This occurrence of EAR corals is used as a potential marker of the Kačák event.

The major facies change occurring at the interface between the Hanonet Fm. (argillaceous fine-grained limestone) and Trois-Fontaines Fm. (massive coarse-grained crinoidal limestone) is probably related to a long-term change of climate change from humid to drier after a short but hot and wet period during the event itself as suggested by Marshall *et al.* (2007).

Acknowledgements

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Appendix. Location of the different sampled localities (see Fig. 2) – [outcrop ID of the Belgian Geological Survey].

1. Mont de Baileux quarry and outcrops (Baileux zoning) N of Baileux – 50° 02´ 26″ N, 4° 23´ 35″ E and 50° 02´ 16″ N, 4° 23´ 04″ E.
2. La Couvinoise (or Haine) quarry in Couvin – 50° 03´ 37″ N, 4° 29´ 25″ E [5780578].
3. Tienne Sainte-Anne (Nismes) – 50° 04´ 06″ N, 4° 33´ 05″ E [5850449].
4. Fond des Vaux sections (Wellin) – from 50° 05´ 27″ N, 5° 06´ 56″ E to 50° 05´ 36″ N, 5° 07´ 03″ E [5960632-33].
5. Resteigne disused quarry – 50° 05´ 24″ N, 5° 10´ 35″ E [5960606].
6. Jemelle quarry – 50° 16´ 44″ N, 5° 26´ 73″ E [5931006].
7. Hampteau disused quarry – 50° 15´ 35″ N, 5° 27´ 53″ E [5550464].