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Lower and Middle Famennian (Upper Devonian) rugose corals from southern Belgium and northern France

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ABSTRACT. After the late Frasnian extinctions, the rugose corals slowly recovered during the Lower and Middle Famennian (*crepida* to *marginifera* conodont zones) in southern Belgium and northern France (Avesnois) (Namur–Dinant Basin). Six genera represented by seven species are recognized and described here; one species (*Breviphrentis superstes*) is new. The rugose coral fauna described herein includes small solitary forms belonging to the so-called *Cyathaxonia* fauna and is similar or very close to those previously described within the same stratigraphic interval in Australia, China and Germany. It also contains a large species belonging to the genus *Breviphrentis* which was considered as extinct since the end of the Givetian (Middle Devonian) ("Lazarus taxon"). The tabulate corals from the Lower and Middle Famennian of this area, mainly represented by auloporids, are also briefly discussed. Rugosa only constituted a minor part of the fauna after the end-Frasnian crisis in the Namur–Dinant Basin contrary to the brachiopods, which were abundant and relatively diversified, and no rugose corals have been recovered from the early Lower Famennian (*triangularis* Zone). The first important Famennian coral radiation only took place during the Latest Famennian (Strunian).

KEYWORDS: Rugosa, Tabulata, *Breviphrentis*, *Cyathaxonia* fauna, post-extinction diversification.

1. Introduction

On a worldwide scale, the Lower and Middle Famennian (Upper Devonian; *triangularis–marginifera* conodont zones) is almost devoid of corals. This is one of the numerous consequences of the Late Frasnian mass extinction that drastically affected the rugose and tabulate corals (e.g. Sorauf & Pedder, 1986; Poty, 1999; Copper, 2002). Their decline was a progressive phenomenon (Poty & Chevalier, 2007; Poty et al., 2011), as was the case for the brachiopods (Mottequin & Poty, 2007, 2008). It started in the Lower *rhenana* conodont Subzone, before the Lower Kellwasser Event, and was practically completed in the Upper *rhenana* Subzone, before the Upper Kellwasser Event that took place during the *linguiformis* Zone.

Very few coral associations were described in Lower Famennian strata (Germany: Weyer 1991, 2004; China: Soto & Liao, 2002; Australia: Hill & Jell, 1971). They usually correspond to the *Cyathaxonia* Fauna constituted of small solitary non-dissepimented corals. These associations are rarely diversified and the corals are usually not abundant, witnessing unsuitable environments.

This paper is the first comprehensive systematic study of the Lower and Middle Famennian rugose corals from southern Belgium and northern France (Fig. 1) which have been considerably less investigated than those of Frasnian age. Until the recent attempts to precise their diversity (Poty, 1986, 1999; Mottequin et al., 2011), they were only known by lists of species devoid of illustrations, which dated back to the second half of the 19th century and which erroneously included species from the shaly formations of Upper Frasnian age (Dewalque, 1868; Gosselet, 1879, 1887, 1888; Mourlon, 1881). On the contrary, due to their greater abundance, their counterparts of the uppermost part of the Famennian (Strunian) have received much more attention (e.g. Haime in Hébert, 1855, Gosselet, 1880; Salée, 1913; Dehée, 1929; Poty, 1986, 1999; Denayer et al., 2011).

2. Geological setting

The studied material is from nine localities belonging to the Namur and Dinant synclinoria, the Vesdre Area and the Theux Window (Fig. 1; see also Appendix 1). These Variscan structural elements constituted the Namur–Dinant Basin, which developed along the southeastern margin of Laurussia during the Devonian and the Carboniferous. The material is from three formations that are briefly described below.

The Famennian (Fig. 2) is particularly well-developed and exposed in the Dinant Synclinorium, from its south-western part in the Avesnes area (northern France) to its north-eastern extension in the East of Belgium. It is mainly composed of predominantly siliciclastic sediments with some calcareous intercalations. The depositional setting approximately corresponds to a ramp with an accentuation of the marine influence and a deepening southwards (Thorez et al., 2006). Therefore, the northern proximal facies, which frequently show a continental influence, are dominantly sandy, silty and shaly, whereas the southern distal facies are dominantly shaly with some calcareous intercalations.

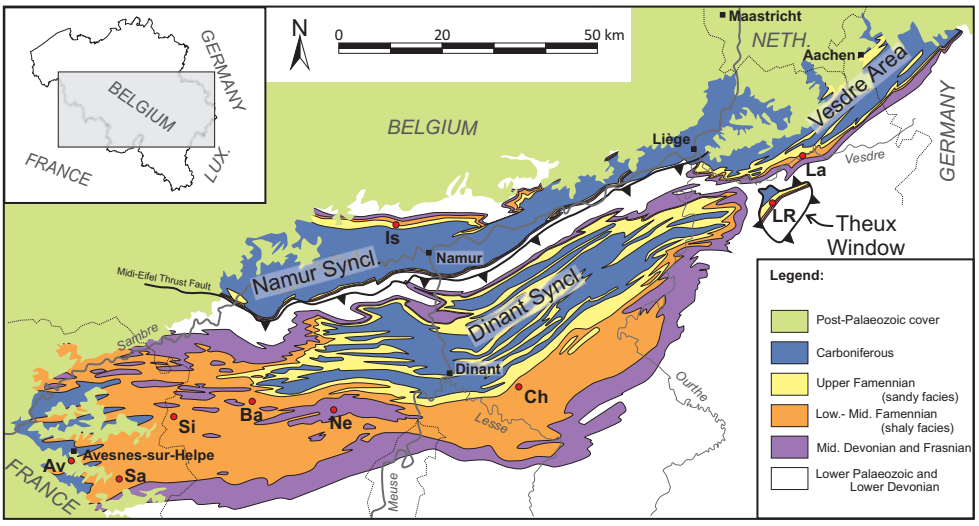

Figure 1. Simplified geological map of southern Belgium and surrounding areas, including the Avesnois (northern France). The red points localize the sampled localities. Legend; Av: Avesnelles and Avesnes-sur-Helpe; Ba: Badon; Ch: Chevetogne; Is: Isnes-les-Dames (Les Isnes); La: Lambermont; LR: La Reid; Ne: Neuville; Sa: Sains-du-Nord; Si: Sivry.; ; NETH.: The Netherlands.

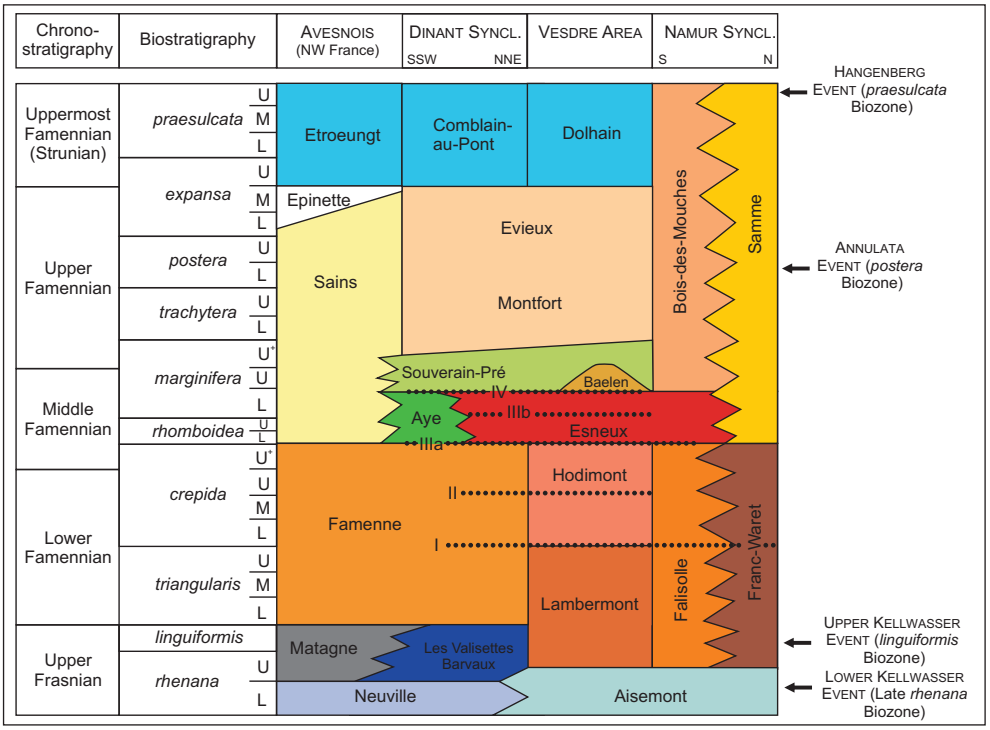

Figure 2. Simplified lithostratigraphical scheme of the Famennian in different tectonic units of southern Belgium, incorporating the Avesnois (northern France) (modified from Thorez et al. (2006) and Delcambre & Pingot (2000, 2008)). Black dotted lines correspond to oolitic ironstone levels (see Dreesen 1982). Syncl.: Synclinorium.

In the Belgian part of the Dinant Synclinorium, deposits of the Lower and of the lower part of the Middle Famennian are almost exclusively argillaceous and are included in the Famenne Group. From the base of the middle part of the Middle Famennian, they pass to the siltstones and sandstones of the Esneux Formation, except in the southern part of the synclinorium where the shales remain predominant and correspond to the Aye Formation (Fig. 2). From the base of the upper part of the Middle Famennian, both formations, which are devoid of corals due to unfavourable facies, pass to the nodular shaly and silty limestones of the Souverain-Pré Formation. The transition between the Aye–Esneux formations and the Souverain-Pré Formation is clearly diachronous, the latter is younger northwards and where it is very weakly developed or even missing.

In the most south-western part of the Dinant Synclinorium, e.g. the southern part of the Avesnes area, which corresponds to the most distal facies, the deposits remain argillaceous (Famenne Group and Sains Formation), but an unit of calcareous shale and shaly limestone beds occurs within the Sains Formation, and laterally correspond to the Souverain-Pré Formation.

The carbonated levels of the Souverain-Pré (Bouckaert & Dreesen, 1977; Poty, 1999; Marion & Barchy, 2004) and of the Sains formations (Poty, 1999; Thorez et al., 2006), that yielded corals, belong to the Upper *marginifera* Subzone (late Middle Famennian). However, the Sains Formation extends from the Lower *rhomboidea* Subzone (middle part of the Middle Famennian) to the Lower–Middle *expansa* subzones (upper part of the Upper Famennian) according to Thorez et al. (2006), and its levels rich in corals were previously assigned to these subzones by Poty (1999).

In the Vesdre Area and the Theux Window, the lowermost part of the silty and shaly Hodimont Formation yielded small solitary non-dissepimented rugose corals, which were collected from the carbonate and shaly beds immediately above an oolitic ironstone level (Dreesen's level I, 1982). The latter corresponds to a condensation horizon comprising at least the Upper *triangularis* and the Lower *crepida* subzones (Dreesen, 1982). Only very uncommon, small and poorly preserved rugose corals were found in the rest of the Hodimont Formation.

On the southern flank of the Namur Synclinorium, rugose corals are known from an oolitic ironstone marker bed that occurs within the Lower Famennian part of the shaly Franc-Waret Formation.

The geological and geographical data of the sampled localities (Fig. 2) are placed in the Appendix 1.

3. Systematic palaeontology

Except two corals coming from the old collection of the University of Liège, all the material investigated was collected by the authors and is deposited in the collections of the Palaeontology Unit of the Liège University (PAULg). The material is listed by locality in Appendix 2. Abbreviations used in the text are as follows: l.s., longitudinal section; t.s., transverse section.

Family Breviphyllidae Taylor, 1951

Genus *Breviphrentis* Stumm, 1949

Type species. Amplexus invaginatus Stumm, 1937, Nevada Limestone, Emsian, Atrypa Peak near Eureka, Nevada.

Diagnosis. See Hill (1981), Oliver (1998), and Pedder (2002).

Discussion. As stated by Stumm (1949), Hill (1981), Oliver (1992) and Pedder (2002; see this author for the synonymies and the species assigned to *Breviphrentis*), the genera *Breviphrentis* Stumm, 1949 and *Breviphyllum* Stumm, 1949 are closely related, and *Breviphyllum* would differ from *Breviphrentis* by the presence of dissepiments and the lack of calicinal expansions (Pedder, 2002). *Breviphrentis* is a relatively well-known genus, which was revised by Oliver (1992, 1998) and Pedder (2002) but *Breviphyllum* remains relatively enigmatic and badly needs a revision as suggested by both authors. Oliver (1998) and Pedder (2002) considered that the presence of septa composed of coarse monacanthine trabeculae and calicinal expansions are characteristic of *Breviphrentis*, which mainly includes species from the Emsian of Western North America. Oliver (1998) established the genus *Contophrentis* for Givetian species from Eastern America previously assigned to *Breviphrentis* but devoid of these characters; its type species is *Zaphrentis halli* Milne-Edwards & Haime, 1851 (*Breviphrentis halli* (Milne-Edwards & Haime) in Oliver, 1993) from the Middle Devonian of the Skaneateles Lake, New York.

Our Famennian specimens have calicinal expansions linked to constriction–rejuvenescence cycles, a character considered as diagnostic for *Breviphrentis* in the literature, but which is typically due to ecological variations and therefore without any taxonomic value. They have lonsdaleoid dissepiments, a character diagnostic for *Breviphyllum*, *Breviphrentis* having not. Nevertheless, these dissepiments are

only developed in the calice during the constrictions, but not during the rejuvenescences, and they do not form a vertically continuous dissepimentarium. Similar development of the dissepimentarium related to constriction and rejuvenescence was described in *Catactotoechus instabilis* (Berkowski, 2012). Their septal microstructure is relatively variable, partly because of their diagenesis, showing well-defined (coarse?) monacanthine trabeculae or not, the presence of coarse monacanthine trabeculae being another character of *Breviphrentis*. Therefore, and although we consider that the relations and differences between

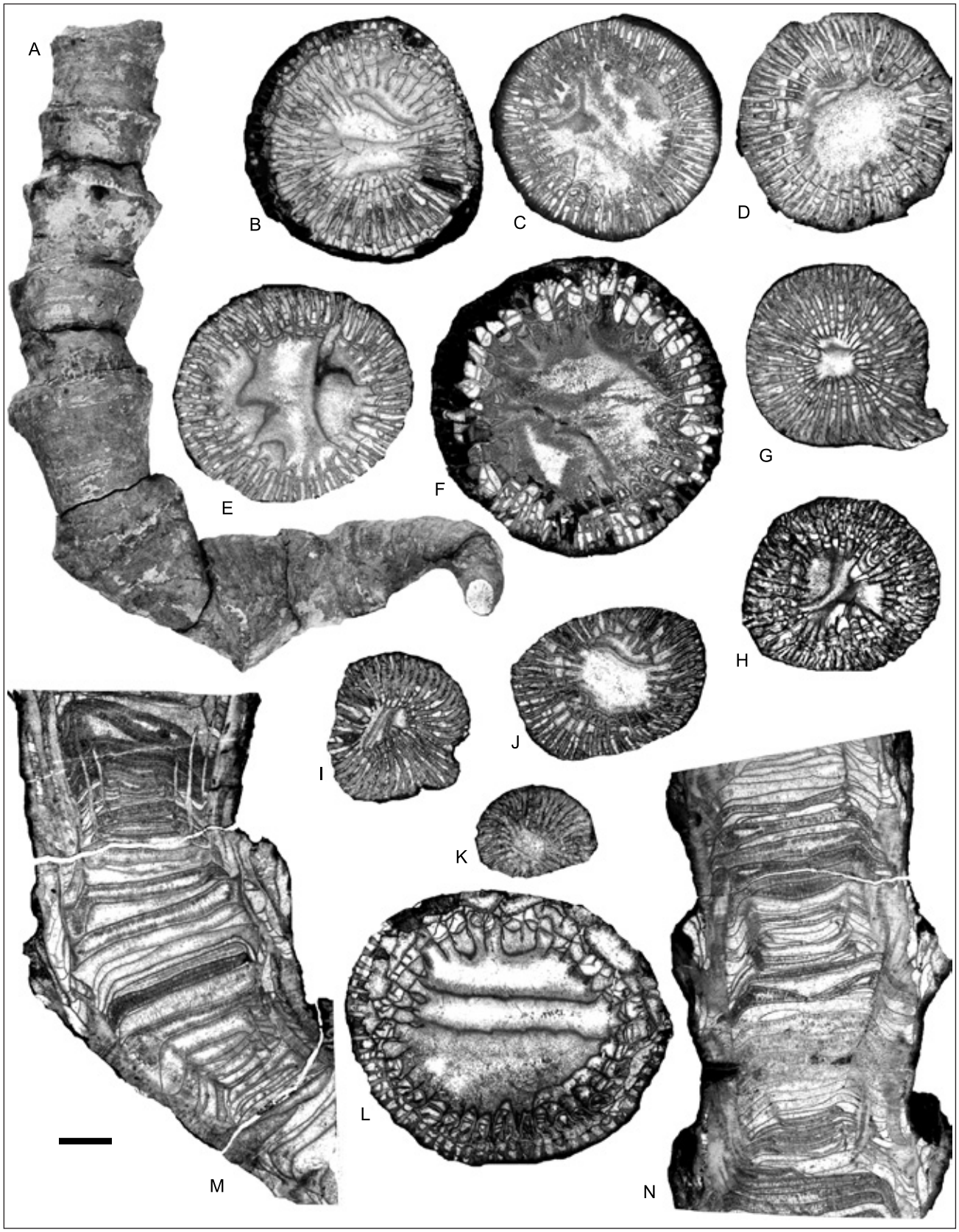

Figure 3. Holotype of *Breviphrentis superstes* sp. nov. Poty & Denayer. Specimen PAULg-S-d-N/6 from the lower part of the Sains Formation, probably Upper *marginifera* conodont Subzone, Sains-du-Nord, Avesnois, North France; sections a to o, successive sections from the top to the base of the coral. A: View of the specimen showing a scolecoid habitus and strong constrictions and rejuvenescences. B: Transverse section 6a. C: Transverse section 6b. D: Transverse section 6d. E: Transverse section 6i. F: Transverse section 6e. G: Transverse section 6j. H: Transverse section 6k. I: Transverse section 6n. J: transverse section 6m. K: transverse section 6o. L: Transverse section showing lonsdaleoid dissepiments due to a constriction phase. 6h. M: Longitudinal section 6g'. N: Longitudinal section 6c showing constrictions and rejuvenescences. A: x1, scale bare: 10 mm. B-N: x2, scale bar : 5 mm.

Breviphrentis, *Breviphyllum*, and *Contophrentis* remain unclear, the Famennian specimens are assigned here to *Breviphrentis*.

***Breviphrentis superstes* sp. nov. Poty & Denayer**
(Figs 3, 5)

Derivation of name. Superstes - to survive - by reference to the reappearance of the genus which was not recorded at least from the Givetian, but indeed survived the Taghanic and the Late Frasnian crises.

Holotype. PAULg-S-d-N/6 (15 t.s., 3 l.s.).

Type locality and horizon. Railway cutting north of the Sains-du-Nord station, Avesnois (northern France) (see Appendix 1); lower part of the Sains Formation, probably Upper *marginifera* conodont Subzone.

Material. Besides the holotype, 24 additional specimens from the same level and area (see Appendix 2).

Diagnosis. Breviphrentis with a mature stage varying between 17–38 mm in diameter and having 31 to 53 major septa (Fig. 4). Major septa sometimes split longitudinally and usually prolonged by a septal lamella. Minor septa relatively long, contratingent or contraclinent. Lonsdaleoid dissepiments present in constricted parts of the coral.

Description. The corallum is usually ceratoid, sometimes trochoid, in the young stages, and becomes cylindrical in mature stages, sometimes scolecoid after toppling over. It has regular periodic constrictions giving up calicinal expansions and rejuvenescences (Figs 3A, 5A, 5O). Each constriction–rejuvenescence cycle is between 15 and 35 mm long. The longest corallum observed reaches a length of 18 cm and shows 8 cycles (Fig. 3A). All our specimens died during constrictions. Three parricidal buds are present in one specimen.

In transversal sections, the youngest stages observed (17 to 23 major septa and 4.3 to 7.5 mm in diameter; Figs 5M, 5P), show irregularly pinnately connected septa reaching 0.5-0.7 mm in thickness, the cardinal fossula is not well-marked, some very short minor septa can be present. From sections with 21 to 23 major septa and 6.5 to 7.0 mm in diameter (Figs 5H, 5I), the major septa lost their connection and withdraw from the axis, and minor septa are well-developed.

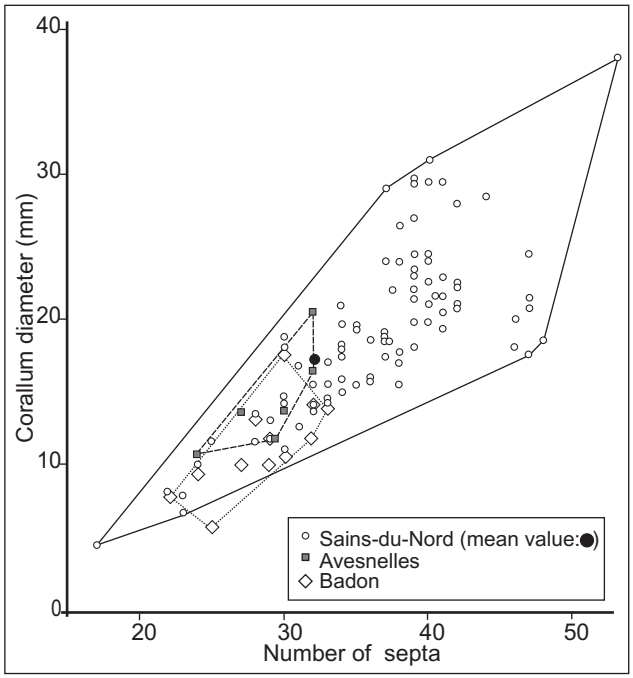

Figure 4. Plot of number of septa versus corallum diameter for *Breviphrentis superstes* sp. nov. Poty & Denayer (specimens from Sains-du-Nord and Avesnelles) and *B.* cf. *superstes*. (specimens from Badon).

The cylindrical parts of the corals have diameters varying from 17–20 mm to 30–38 mm and 30 to 53 major septa The number of septa does not decrease during constrictions. The major septa extend for 1/4 to 4/5 of the radius and they never reach the axis. They are short to long, straight to sinuous, sometimes split by the development of lateral vesicules or terminated by a inner fork. They can be slightly rhopaloid, and their thickness varies from 0.4–0.7 mm at their base to 0.1–0.3 mm in their medium part and to 0.3–0.4 mm at their inner end which are often prolonged by a whip-like septal lamella. The minor septa are relatively long with regard to the major ones, reaching 1/3 to 4/5 of their length (1/4–1/3 of the radius). They are contraclinant and sometimes contratingent, their thickness can reach 0.8 mm. The septa can be a little more thickened in the cardinal quadrants than in the counter ones. A cardinal fossula is inconspicuous to well-marked, with a short cardinal septum. The counter septum is not well differentiated from the others. Lonsdaleoid dissepiments are present in some transverse sections. The outer wall is usually not well-preserved and its thickness varies from 0.5 to 1.5 mm.

In longitudinal sections (Figs 3M, 3N, 5R), tabulae are complete to slightly divided; they are flat to moderately concave and decline outwards to form a peripheral, sometimes deep, gut. The width of the axial elevated part of the tabulae decreases during constrictions and enlarges during rejuvenescences. The space between tabulae in the axial part varies between 0.1 to 2 mm. Dissepiments are formed during each constriction of the corallum, diminishing the internal diameter of the calice. They do not form a continuous dissepimentarium and do not develop during rejuvenescences.

Discussion. Due to wide variations in morphology and size, some specimens of *B. superstes* sp. nov. resemble to species known from the Lower and Middle Devonian:

B. invaginata, the type species of *Breviphrentis* from the Emsian of Nevada (see its revision by Oliver, 1992) is 18–22 mm in diameter with 37–46 major septa, but its major septa are usually longer, more dilated at periphery than in *B. superstes*, and forming a septotheca.

Contophrentis halli (Milne-Edwards & Haime, 1851), from the Givetian, Staghorn Point coral bed, New York (40 to 63 major septa in sections having diameters of 30 to 50 mm) is close to *B. superstes*, but its septa are a little longer and thicker that in our specimens.

Contophrentis cista Oliver, 1992, Givetian, Staghorn Point coral bed, New York, has a size similar to that of our specimens (20–40 mm, reaching 50 mm and 40 to 58 major septa in sections having diameters of 25 to 50 mm), but differs by its shorter minor septa, its tabulae thickened and widely spaced with their axial part strongly concave.

Contophrentis pumilla Oliver, 1992, Givetian, Centerfield Member, Ludlowville Formation, Hamilton Group, western New York, is smaller, 13–18 mm in diameter, with 24–32 major septa.

Moreover, the new species can be easily distinguished by its major septa affected by splitting and their inner end prolonged by septal lamellae which are not known in other species of this group.

Distribution. B. superstes sp. nov. (= *B.* sp. B in Poty, 1999) is only known from the lower part of the Sains Formation in the Avesnes area. Note that Gosselet (1880, p. 547) reported corals in the same stratigraphic levels in the railway cutting north of the Sains-du-Nord station, that he assigned to *Clisiophyllum omaliusi* Haime (*in* Hébert, 1855). Haime's species was never observed below the Uppermost Famennian (Strunian) and Gosselet (1880) probably mistook it with our new species.

***Breviphrentis* cf. *superstes* sp. nov.**
(Fig. 6)

Material. Six specimens from Badon and four from Sivry (see Appendix 2).

Description. The corals are small and cylindrical, with a diameter of 10 to 17 mm and 25 to 30 major septa in mature stages. They can

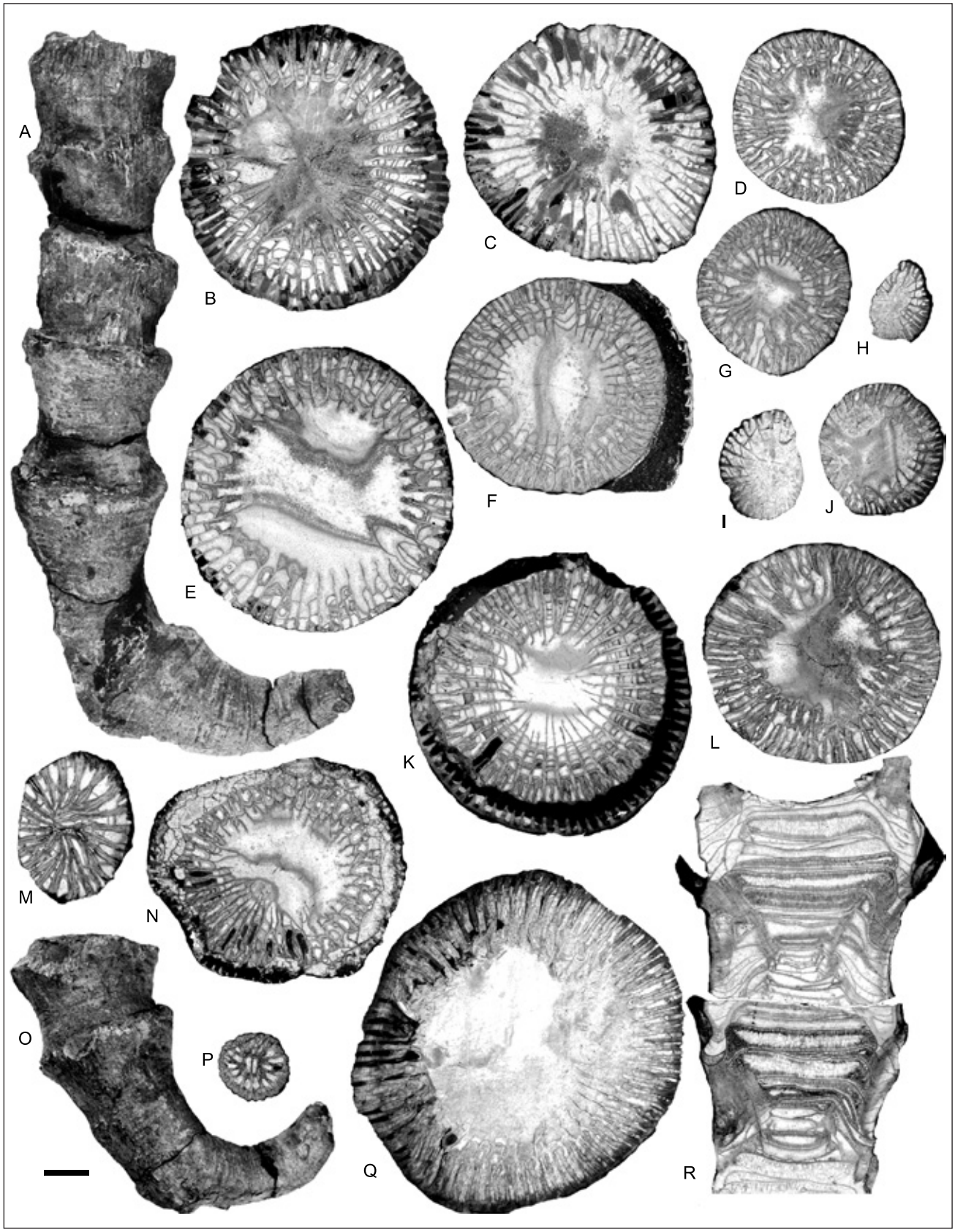

Figure 5. *Breviphrentis superstes* sp. nov. Poty & Denayer. A-J, L: Specimen PAULg-S-d-N/14 from the lower part of the Sains Formation, probably Upper *marginifera* conodont Subzone, Sains-du-Nord, Avesnois, North France. A: View of the specimen showing a toppling over, strong constrictions and rejuvenescences. B: Transverse section 14a. C: transverse section 14b. D: Transverse section 14h. E: Transverse section 14g. F: Transverse section 14f. G: Transverse section 14o. H: Transverse section 14n. I: Transverse section 14q. J: Transverse section 14p. L: Transverse section 14m. K: Specimen PAULg-S-d-N/17 from the lower part of the Sains Formation, Sains-du-Nord. K: Transverse section 17d showing calicinal a expansion due to a constriction phase. M: Specimen PAULg-S-d-N/9 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 9d in a young stage showing pinnately connected septa. N: Specimen PAULg-S-d-N/15 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 15b showing lonsdaleoid dissepiments formed during a constriction phase. O: Specimen PAULg-S-d-N/9 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 9d. P: Specimen PAULg-Avesnes-VII-2 from the lower part of the Sains Formation, Avesnes-sur-Helpe, Avesnois, North France, transverse section IIg in a young stage showing pinnately connected septa. Q: Specimen PAULg-S-d-N/5 from the lower part of the Sains Formation, Sains-du-Nord, transverse section 5a. R: Specimen PAULg-S-d-N/10 from the lower part of the Sains Formation, Sains-du-Nord, longitudinal section 10b showing strong constrictions and rejuvenescences. A, O: x1; B-L, N, Q-R: x2, scale bar : 5 mm, except A, N: 10 mm and M, P: 2.5 mm.

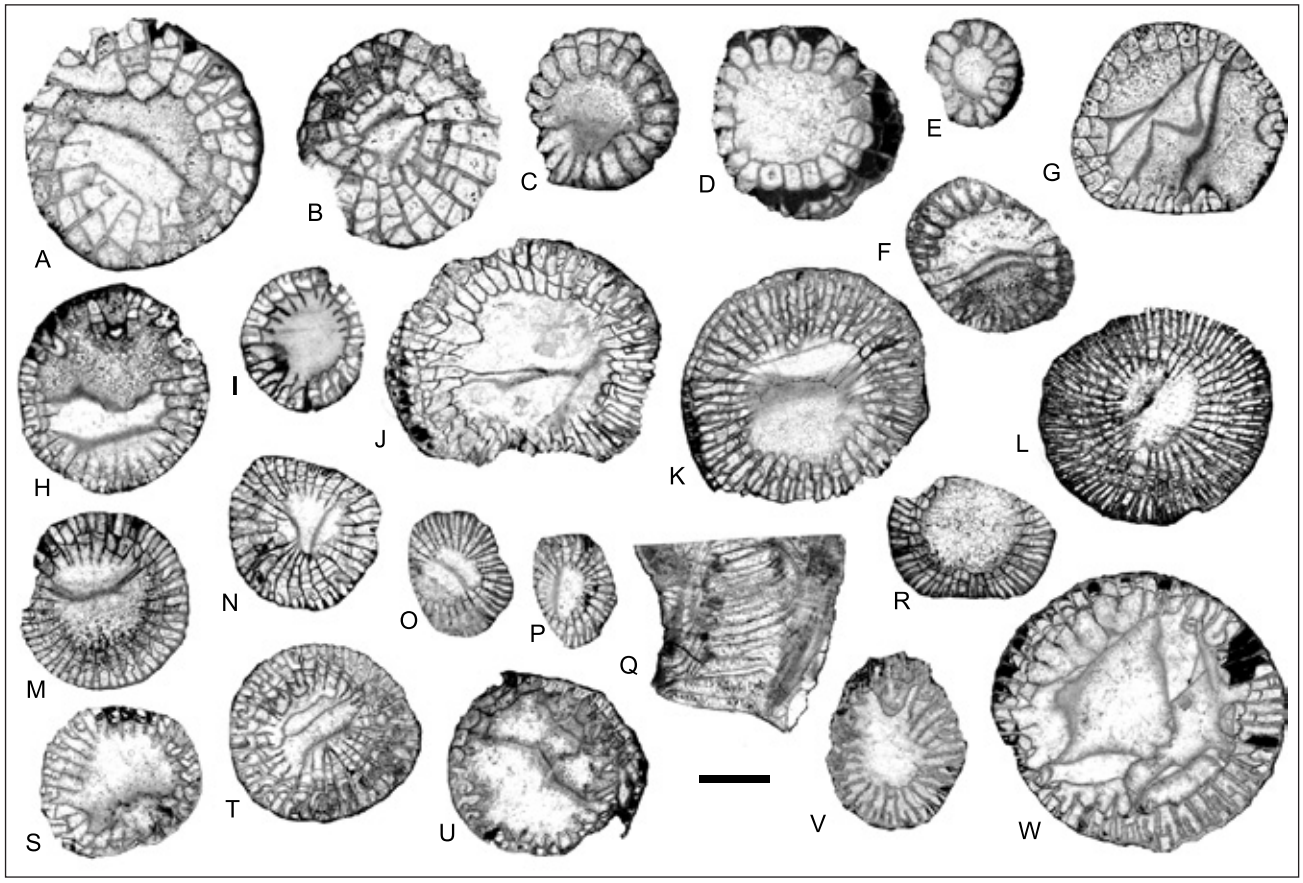

Figure 6. A-B, F-W: *Breviphrentis* cf. *superstes* sp. nov. Poty & Denayer. A: specimen PAULg-Sivry 66B/II from the Souverain-Pré Formation, Sivry, Belgium, transverse section IIa. B: Specimen PAULg-Sivry 66B/IV, transverse section IVa. F: Specimen PAULg-Badon/2 from the Souverain-Pré Formation, Badon, Belgium, transverse section 2b. G-H, N: Specimen PAULg-Badon/9, G: Transverse section 9c. H: Transverse section 9b. N: Transverse section 9e. I: Specimen PAULg-Badon/5, transverse section 5a. J-M, O-R: Specimen PAULg-Avesnes 50/75 from the Sains Formation, Avesnes-sur-Helpe, Avesnois, North France. J: Transverse section b. K: Transverse section c. L: Transverse section d. M: Transverse section f. O: Transverse section h. P: Transverse section i. Q: Longitudinal section e. R: Transverse section g. S-W: Specimen PAULg-Avesnes 57/50 from the Sains Formation, Avesnes-sur-Helpe, Avesnois, North France. S: Transverse section e. T: Transverse section d. U: Transverse section f. V: Transverse section g. W: Transverse section b. C-E: *Catactotoechus* sp. from the Souverain-Pré Formation (Upper *marginifera* Subzone), specimen PAULg-Chev.1993/1/I from, Chevetogne, Belgium. C: Transverse section Ic. D: Transverse section Ib. E: Transverse section Id. A-F: x4, scale bar : 2.5 mm, G-W: x2, scale bar: 5 mm.

show constrictions and rejuvenescences. The longest specimen is 5 cm long. The major septa are thin to thick, and extend for 1/4 to 2/3 of the radius. The minor septa are short, sometimes contraclinant or contratingent. The tabulae are complete to slightly divided, flat to moderately concave, and decline outward to form a peripheral gut. The width of the axial elevated part of the tabulae decreases during constrictions and enlarges during rejuvenescences. There are no dissepiments. Juvenile stages were not observed.

Discussion. The transverse sections of these small corals are identical to those of young stages of *Breviprentis superstes* sp. nov. having the same diameter. Their longitudinal sections share similarities with those of *B. superstes*. These specimens may probably correspond to dwarf specimens of the latter and probably lived in ecological conditions not so favourable than those prevailing in the environment where *B. superstes* occurred, as the material from Sivry and Badon is from the Souverain-Pré Formation, which is represented mainly by sandy and argillaceous packstones and wackestones.

Distribution. Breviphrentis cf. *superstes* sp. nov. (= *B.* sp. A in Poty (1999) is known from the Souverain-Pré Formation in the southwestern part of the Dinant Synclinorium (Badon and Sivry sections). In Sivry, it is associated to spire-bearer (spiriferids and athyridids), orthid and rhynchonellid (*Centrorhynchus letiensis* group) brachiopods.

Family Laccophyllidae Grabau, 1928

Genus *Catactotoechus* Hill, 1954

Type species. Catactotoechus irregularis Hill, 1954, Famennian, *Spinulicosta proteus* Zone, Fairfield Formation, Oscar Hill, Canning Basin, NE Australia.

Discussion. The genus *Hillaxon* Różkowska 1969, from the Famennian of Poland is possibly a junior synonym.

***Catactotoechus* sp.**
(Fig. 6 C-E)

Material. two specimens from Chevetogne, Souverain-Pré Formation, upper *marginifera* Subzone.

Description. Small solitary subcylindrical coral 6.2 to 8.0 mm in diameter with 20 to 25 major septa. The major septa extend for 1/3 to 3/5 of the radius and are more or less sinuous. There are no minor septa. The cardinal fossula is inconspicuous. An aulos is present in sections of 3.5 and 4.0 mm in diameter with 16 major septa and disappears from sections of 6.2–6.5 mm in diameter with 20–24 major septa. Its diameter is above 0.4 of the diameter of the coral. Some single dissepiments develop from a section of 6.5 mm in diameter and form three incomplete series in the wider section observed (8.0 mm in diameter). The outer wall is 0.1–0.2 mm thick. Characters in longitudinal section were not observed.

Discussion. Both specimens clearly belong to the genus *Catactotoechus*, but until larger collections, it is advisable to leave them unnamed.

Distribution. *Catactotoechus* sp. is only known from the Souverain-Pré Formation (Upper *marginifera* Subzone) in the

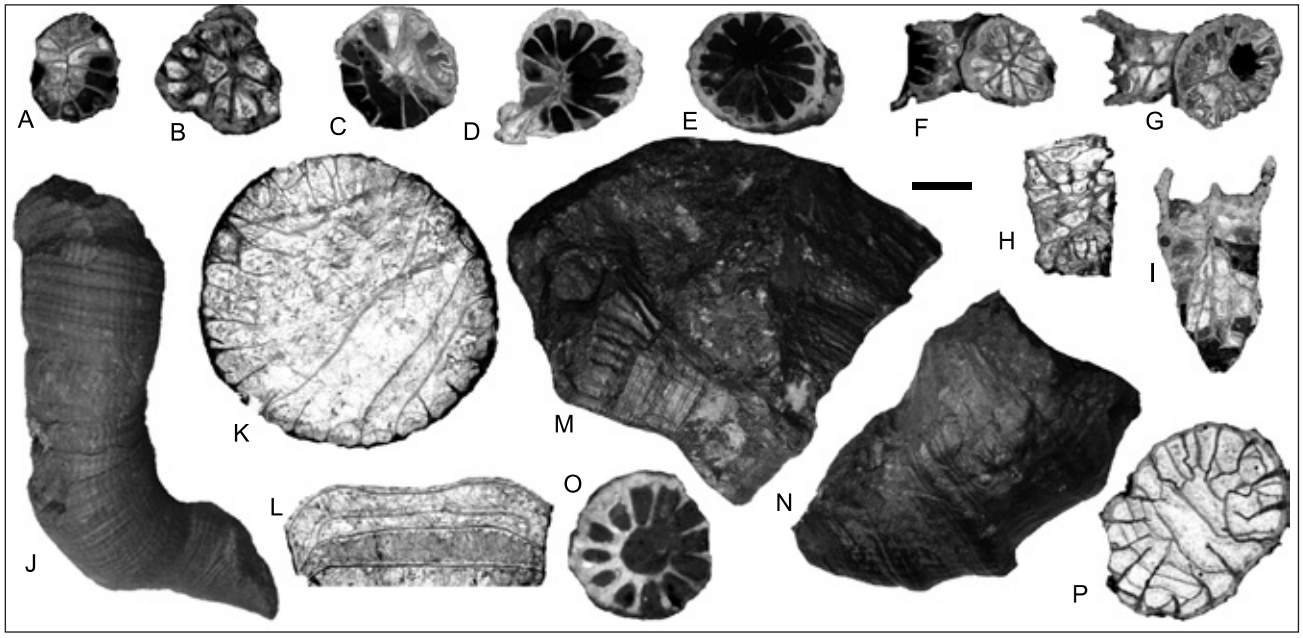

Figure 7. A-I: *Cheilaxonia* cf. *hofmanni* Weyer, 2004, from the base of the Hodimont Formation (Lower *crepida* Subzone), Lambermont section, Belgium. A: Specimen PAULg-Lamb.17/XXXVIII, transverse section. B: Specimen PAULg-Lamb.18/LV, transverse section. C: Specimen PAULg-Lamb.13/XI, transverse section. D: Specimen PAULg-Lamb.13/XII, transverse section. E: Specimen PAULg-Lamb.11/IV, transverse section. F: Specimen PAULg-Lamb.17/XXXIX., transverse section. G: Specimen PAULg-Lamb.15/XXVIII, transverse section. H: Specimen PAULg-Lamb.12/III, longitudinal section. I: Specimen PAULg-Lamb.11/I, longitudinal section. J-L: *Amplexus* sp., specimen PAULg-Isnes/dec.2011/I from the oolitic ironstone level I of the Franc-Waret Formation (Lower *crepida* Subzone) from the Isnes-les-Dames iron mine. J: View of the specimen showing a scolecoid habitus and growth ridges. K: Transverse section Ic. L: Longitudinal section Id. M-N: *Tabulophyllum* ? sp. specimen PAULg-Isnes/dec.2011/II from the oolitic ironstone level I of the Franc-Waret Formation (Lower *crepida* Subzone) from the Isnes-les-Dames iron mine. M: View of the sample showing 2 gregarious (?) specimens. N: View of the specimen showing growth ridges. O: *Neaxon* sp., specimen PAULG-Lamb.12/I form the base of the Hodimont Formation (Lower *crepida* Subzone), Lambermont section, Belgium, transverse section. P: Gen. et sp. unknown, specimen PAULg-Neuville 2012/VI/1 from the limestone level forming the base of the Matagne Formation (*linguiformis* Zone, Upper Frasnian), Neuville railway section, Belgium. J and M-N: x2, scale bar: 4 mm. A-I, K-L and P: x4, scale bar: 2 mm. O: x8, scale bar: 1 mm.

Chevetogne section (see Appendix 1). The genus is also known in the Famennian of Australia (Hill & Jell, 1971), in the Frasnian of northern France (Rohart, 1988) and from the Emsian of Morocco (Berkowski, 2008).

Family Protozaphrentidae Ivanovskiy, 1959

Genus *Cheilaxonia* Weyer, 2004

Type species. Cheilaxonia hofmanni Weyer, 2004, Lower Famennian (Middle–Upper *crepida* subzones), Thüringisches Schiefergebirge, Germany.

***Cheilaxonia* cf. *hofmanni* Weyer, 2004**
(Fig. 7A-I)

Material. Sixty-five specimens badly preserved, crushed, bored and abraded from the base of the Hodimont Formation (Lower *crepida* Subzone) Lambermont section and several uncut specimens from the "Heid de Fer" section near La Reid (see Appendix 1).

Description. Our specimens are often found attached on each other by short outgrowth, proving a gregarious way of live. Consequently, their skeletal elements are deformed, and are often oval in section. The diameter varies from 2.5 to 7 mm. There are 12 to 16 (max. 18) septa, commonly curved and fusing in clusters of 2–4 before joining the axis. They form a weak axial structure in which cardinal and counter septa are almost always implied with several other major septa. The latter are not thickened, except near the wall. The cardinal and counter septa are slightly thicker where implied in the axial structure. The minor septa are absent in sections smaller than 4 mm and remain short in larger calicular sections. All the septa tend to withdrawn from the axis in the calice. Some rare simple dissepiments are present in the larger calicular sections. The wall is thick (0.1–0.3 mm) and undulating or festooned. The tabulae are flat in the axial zone and slightly declined outwards.

Discussion. The weak axial structure formed by the axial ends of the septa and the septa arranged in clusters near the axis of the corallite are the diagnostic character of the genus *Cheilaxonia* Weyer, 2004. The morphology of the Belgian material is close to the small undissepimented coral *Metriophyllum* Milne-Edwards & Haime, 1850, but the latter commonly shows small septal spines. Our corals show many common points with *Petraiella reichsteini* described by Weyer (1991) from the Lower Famennian limestone capping the Devonian Iberg Reef in the Harz Mountains. Dimensions and number of septa are comparable, as well as the curved septa but the axial structure is more developed in the Belgian corals. Nonetheless, our material displays the same characters and size than the type material of *C. hofmanni* from the Lower Famennian strata of Thuringia illustrated by Weyer (2004). However, the poor state of preservation precludes the definite specific identification.

Distribution. The small solitary undissepimented rugose corals identified as *Cheilaxonia* cf. *hofmanni* are known from the base of the Lower Famennian Hodimont Formation (Lower *crepida* Subzone) in the Vesdre Area (Lambermont) and the Theux Window (La Reid) (eastern part of Southern Belgium). In the Lambermont section (Vesdre Area), the bulk of the specimens was collected in a single bed of green to red argillaceous limestone overlying the oolitic hematite horizon (level I of Dreesen, 1982), which is characteristic of the base of the Hodimont Formation. In this section, additional specimens were also recovered from the base of a shaly bed, which caps the limestone bed described below, and were associated to several specimens of an unidentified species of rhynchonellid brachiopod (Fig. 8). The latter are small-sized and smooth (except the presence of a median furrow on the fold and a low median rib in the sulcus of some shells). However, the lack of knowledge about their internal morphology, because of a lack of material suitable for serial sectioning, prevents an accurate identification.

Family Petraiidae De Koninck, 1872

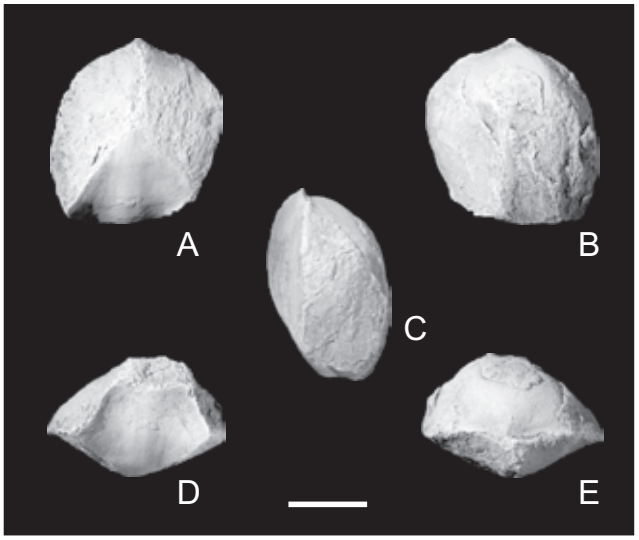

Figure 8. Undetermined rhynchonellid brachiopod (PAULg 2011-11-6) associated with *Cheilaxonia* cf. *hofmanni* Weyer, 2004 and *Neaxon* sp. in the lowermost part of the Hodimont Formation (Lower *crepida* Subzone), Lambermont section, Belgium. A: Ventral view. B: Dorsal view. C: Lateral view. D: Anterior view. E: Posterior view. A-E: x2, scale bar: 5 mm.

Genus *Neaxon* Kullman, 1965

Type species. *Neaxon regularis* Kullman, 1965, Upper Emsian, East of Muda, North Spain.

***Neaxon* sp.**
(Fig. 7 O)

Material. Two incomplete specimens from the Lambermont section (see Appendix 1).

Description. Our specimens are 3 and 4 mm in diameter and show 12 and 16 septa, respectively. The aulos is 0.5 to 0.8 mm in diameter. Wall and septa are at the maximum 0.25 mm-thick. No dissepiments were observed. Neither the external characters nor the longitudinal section are known. The bad preservation of the specimens does not allow further description.

Discussion. The absence of dissepiments excludes our specimen from genera such as *Amplexocarinia* Soskina, 1941 and *Czarnockia* Różkowska, 1969. Furthermore, the absence of contratingent minor septa excludes the attribution to *Syringaxon* Lindström, 1882. Nevertheless, the lack of knowledge about the location of the section through the corallite precludes an accurate specific identification, based on the size and number of septa. *Neaxon regularis*, the type species, is Emsian (Kullmann, 1965), whereas *N. regulus* Weyer, 1971, *N. bartzschi* Weyer, 1978 and *N. muensteri* Weyer, 1989 are Upper Famennian (Weyer, 1971, 1978, 1989). These three species are larger (>10 mm) than the Belgian one. *N. cheilos* Weyer, 1984 is the only species of *Neaxon* described from the Lower Famennian strata (Weyer, 1984). Our specimens could belong to this last species but the material is not sufficiently good to allow a specific attribution.

Distribution. *Neaxon* sp. is only known from the lowermost part of the Hodimont Formation in the Lambermont section, where it is associated to *Cheilaxonia* cf. *hofmanni*.

Family Amplexidae Chapman, 1893

Genus *Amplexus* Sowerby, 1814

Type species. *Amplexus coralloides* Sowerby, 1814, Lower Carboniferous, Limerick, Ireland.

***Amplexus* sp.**
(Fig. 7 J-L)

Material. One single specimen from Isnes-les-Dames iron mine (Les Isnes), housed in the old collection of the Liège university (Dewalque's collection). The specimen is hematitized but some parts of the original carbonated skeleton are preserved.

Description. This specimen is a 4-cm long scolecoid coral, showing two changes in growth direction, partly included in the hematitic rock. Small septal furrows and growth lines are visible on the external wall. The larger cylindrical part of the corallite is 11 mm in diameter and has 25 septa. The septa are very short (0.6–1 mm) and amplexoid. The minor septa are reduced to septal crest on the wall. The wall is 0.1 mm thick and undulating. In the longitudinal section, the tabulae are complete, flat and mesa-shaped, lately plunging towards the periphery. They are regularly spaced and there are 5 tabulae in a section of 5 mm high.

Discussion. Both the external and the internal characters are typical of the genus *Amplexus*. This specimen could be compared to *A.* sp. C from the Lower Famennian of Rübeland figured by Weyer (1991), but the latter specimen is 3 mm-large and shows almost no septa. Our specimen enters in the very large range of variability of the Carboniferous species *A. coralloides* Sowerby, 1814, and could be assigned to this species, but further specimens are needed to support this specific identification.

Distribution. *Amplexus* sp. is from the oolithic hematite horizon which occurs within the Lower Famennian part of the Franc-Waret Formation. This level was intensively mined for iron ores from 1830 to 1940, north of the Meuse Valley between Namur and Liège. This exploitation being hand-made, fossils were from time to time collected and then housed in the Liège University.

Family Endophyllidae Torley, 1933

Genus *Tabulophyllum* Fenton & Fenton, 1924

Type species. *Tabulophyllum rectum* Fenton & Fenton, 1924, Upper Devonian, Iowa.

***Tabulophyllum* ? sp.**
(Fig. 7 M-N)

Material. One sample with six (?) gregarious specimens, hematitized and poorly preserved, from the Isnes-les-Dames iron mine (Les Isnes), housed in the old collection of the Liège University (Dewalque's collection).

Description. This sample is made of three specimens included in the rock, plus at least, three other individuals known by their imprints on the same sample. These six corals seem to have formed a pseudo-colony. The larger specimen is 25 mm high and 16 mm in diameter. Shallow septal furrows and tight growth lines are visible on the external surface of the wall, on all the individuals. The internal structures are almost not preserved from the mineralization, except some fragments of septa and wall in one specimen. Therefore the description is very limited. The estimated number of septa is 28 for a diameter of 10 mm. The septa are sinuous and withdrawn from the axis, leaving a free (?) zone in the centre of the corallite. No minor septa are observed. Several lonsdaleoid dissepiments, arranged in a single (?) row, are visible.

Discussion. The present material is inadequate for a precise identification due to its poor preservation. However, the presence of lonsdaleoid dissepiments suggests the genus *Tabulophyllum*, which is common in the Upper Frasnian and also present occasionally in the Uppermost Famennian (Poty, 1999).

Distribution. Same as for *Amplexus* sp.

4. Stratigraphy and diversity

The stratigraphic range of the rugose corals genera for the considered biostratigraphic interval (*triangularis* Zone to *marginifera* Zone) across the Namur-Dinant Basin is presented in

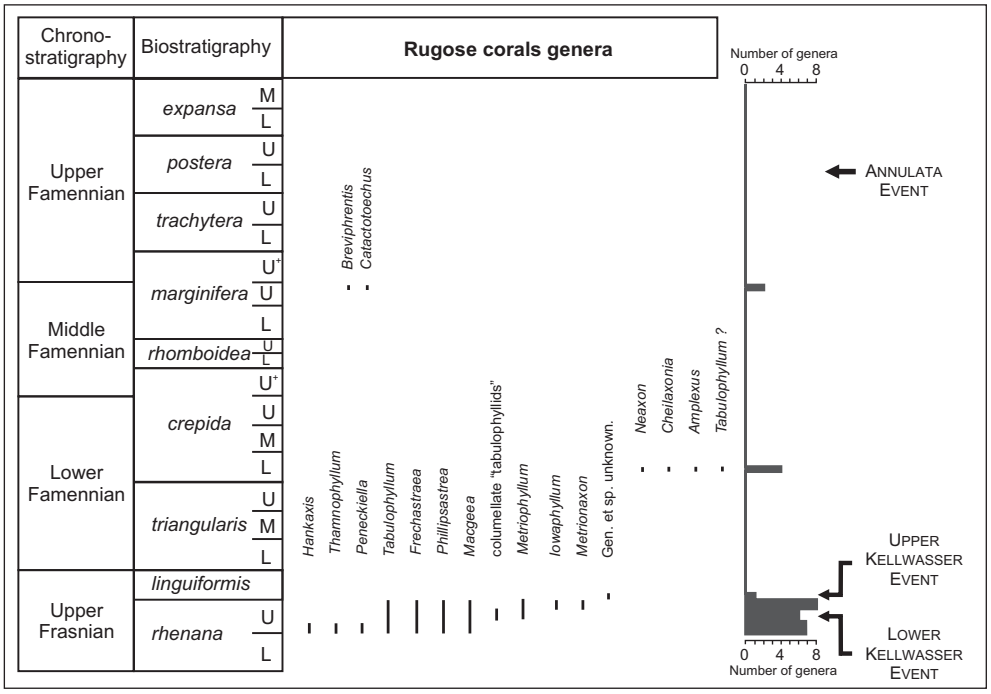

Figure 9. Stratigraphical distribution of the Upper Frasnian and Lower to Middle Famennian rugose corals from southern Belgium and northern France. The diversity curve, in the right part of the figure, clearly shows the extinction preceding the Frasnian/ Famennian boundary. Data from Paquay (2002), Denayer & Poty (2010), Poty & Chevalier (2007), Coen-Aubert (1974, 1982, 2011).

Fig. 9. The Belgian Lower and Middle Famennian rugose corals are only known from two levels as described in the introduction and in the following paragraph.

The diversity curve clearly shows the slow decrease in number of rugose coral genera during the Upper Frasnian and their complete extinction before the Upper Kellwasser Event (Fig. 9). The youngest Frasnian rugose corals of Belgium are very simple small solitary forms, of unknown affinity (Fig. 7 P), found at the top of the Les Valisettes Formation (*linguiformis* Zone (Bultynck et al., 1998)), in the Philippeville Anticlinorium (Neuville new railway section), just below the Upper Kellwasser black shales (Matagne Formation). The diversity of the lower Famennian strata is relatively high with regard to the upper strata (four genera, two of them being represented by single specimens), but there is an artefact due to a more intense exploration of this interval. The Middle Famennian, represented by the Souverain-Pré and Sains formations, yielded abundant but very poorly diversified material including two genera represented by three species. This poor diversity of corals clearly indicates that their post-extinction recovery was not facilitated by unfavourable environments during the Lower and Middle Famennian, long before the Strunian radiation (Uppermost Famennian), the Upper Famennian strata being devoid of corals in Belgium (Poty, 1986).

5. Discussion and conclusions

The rugose coral fauna from the Lower and Middle Famennian of the Namur–Dinant Basin comprises small solitary forms that belong to the so-called *Cyathaxonia* fauna of Hill (1981). This fauna is similar, or closely related, to those described from the Lower-Middle Famennian of China (Soto & Liao, 2002), Australia (Hill & Jell, 1971), Germany (Weyer, 1991, 2004), and the Omolon region in North-East Siberia (Poty, 1986). However, the Siberian fauna was considered as Upper Famennian by Shilo et al. (1984) but could be possibly older (Poty, 1999).

The coral fauna described by Różkowska (1969) in the Famennian of Poland also comprises small solitary corals without dissepiments, close to those described here, and dissepimented solitary and colonial ones. Nonetheless, the Polish coral fauna is difficult to compare with others as some corals were probably reworked from pre-Famennian deposits, and others were misidentified (Poty, 1986, 1999).

The Middle Famennian coral fauna of the Namur-Dinant Basin also includes large solitary rugosa which are assigned to the new species *Breviphrentis superstes* sp. nov. and *B.* cf. *superstes*. The genus *Breviphrentis* was considered as extinct for at least the end of the Givetian, and its brief reappearance during the Famennian qualifies it as a "Lazarus taxon". These corals may have migrated to deep-water-like environments (probably not true deep-water environments where anoxic conditions dominated and had to prevent their development) that permit them to survive at the late Frasnian crisis. They latter reappeared in shallow-water environments during Lower and Middle Famennian but probably became extinct (or migrated again) because of unsuitable conditions during the Upper Famennian times.

As described in the systematic paragraph, the morphology of *Breviphrentis superstes* and *B.* cf. *superstes* is unstable. The inter-individual and ontogenetic variations are very wide and witness the very plastic morphology of these taxa. This plasticity is most probably linked to the very low natural selection pressure conducted by ecological conditions through the mixed siliciclastic-carbonated deposition environment, as signalized for Strunian campophyllids (Poty, 2010). The corals were able to react rapidly to changes of environmental conditions (as shown by the constriction–rejuvenescence cycles) and adapt their morphology in consequence (Scrutton, 1998).

Most of these Lower and Middle Famennian rugose corals became extinct before the first Uppermost Famennian (Strunian) coral radiation which took place in the Upper *expansa* Subzone (Poty, 1999).

Tabulate corals are known from the Lower and Middle Famennian of the Namur–Dinant Basin but are only represented by species belonging to the primitive and long-ranging taxa *Aulopora* and *Cladochonus*. Auloporids were reported in the Lower Famennian Famenne Group by Gosselet (1877, 1888) and illustrated by Mottequin (2008, figs 10.3 and 10.13); *Cladochonus* only occurs in the Souverain-Pré Formation (Chevetogne section). Maillieux (1930) cited syringoporids in the Lower Famennian of southern Belgium, but micheliniids and syringoporids are not known before the Strunian. Note that stromatoporoids, which disappeared at the end of the Frasnian in the studied area, only reoccur during the Strunian, before their total extinction at the end of the Famennian (Hangenberg Event).

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Appendix 1. Geological and geographical data of the sampled localities

- Avesnes. Cemetery street section, (50° 06' 42" N, 3° 57' 25" E) (Conil, unpublished data), Avesnois, North France; Sains Formation.
- Avesnelles. Railway cutting, (50° 06' 47" N, 3° 57' 30" E) (Conil, unpublished data), Avesnois, North France; Sains Formation.
- Badon. Trench of the road Charleroi-Couvin (N5) (50°11'39.59" N; 4°22'46.79") (e.g. Bouckaert & Dreesen, 1977; Dreesen, 1978; Poty, 1999); Souverain-Pré Formation.
- Chevetogne. Access road to the provincial domain of Chevetogne (N 50°13'28.38"; E 5°08'29.46") (Poty, 1999); Souverain-Pré Formation.
- Isnes-les-Dames. Most probably form the old iron mine of Isnes-les-Dames (N50°30'21.73"; E4°43'42.58"), housed of the former palaeontological collections of the University of Liège (Dewalque's collection) ; lower part of the Franc-Waret Formation.
- Neuville. Neuville, south-west of the village, on the eastern side of a trench dug for the Couvin-Charleroi railway (N50°10'00" ; E4°29'53.50") (e.g. Bultynck et al., 1998; Azmy et al., 2012); top of the Les Valisettes Formation.
- Lambermont. Western access road to the highway Verviers-Prüm (N 50°35'40.36"; E 5°50'33.86") (e.g. Dreesen, 1982; Laloux et al., 1996); base of the Hodimont Formation.
- La Reid. Foothpath linking the village of La Reid to the Becco hamlet ("Heid de Fer") (N 50°29'47.28"; E 5°47'23.80"); base of the Hodimont Formation.
- Sains-du-Nord. Railway cutting (50° 05' 34-36" N, 3° 59' 57" E) (Conil, unpublished data), Avesnois, North France; Sains Formation (coral material from the lower part of the formation).
- Sivry. Along the Là-Haut street, north of the village of Sivry (N 50°10'11.68"; E 4°10'51.38") (Marion & Barchy, 2004); Souverain-Pré Formation.

Appendix 2. List of specimens

Breviphrentis superstes Poty & Denayer:
- Sains-du-Nord: S-d-N/1 (1 t.s.), S-d-N/2 (6 t.s.), S-d-N/3 (11 t.s. & 1 l.s.), S-d-N/4 (2 t.s. & 1 l.s.),S-d-N/5 (6 t.s. & 1 l.s.), S-d-N/7 (7 t.s.), S-d-N/8 (4 t.s.), S-d-N/9 (3 t.s. & 1 l.s.), S-d-N/10 (3 t.s. & 1 l.s.), S-d-N/11 (4 t.s.), S-d-N/12 (8 t.s. & 1 l.s.), S-d-N/13 (9 t.s. & 1 l.s.), S-d-N/14 (17 l.s. & 1 l.s.), S-d-N/15 (7 t.s. & 1 l.s.), S-d-N/16 (4 t.s.), S-d-N/17 (13 t.s.), S-d-N/18 (5 t.s. & 2 l.s.), S-d-N/19 (8 t.s.), S-d-N/20 (4 t.s.), S-d-N/21 (2 t.s.), S-d-N/22 (2 t.s. & 1 l.s.), S-d-N/23 (2 t.s. & 1 l.s.), S-d-N/24 (1 t.s. & 1 l.s.), S-d-N/25 (6 t.s. & 1 l.s.).
- Avesnes: A.VII/1 (5 t.s.), A.VII/4 (3 t.s.), A.VII/5 (2 t.s. & 2 l.s.), A.VII/7 (1 t.s. & 1 l.s.).
- Avesnelles: A.50/57 (6 t.s. & 1 l.s.), A.50/74 (4 t.s. & 1 l.s.), A.50/75 (8 t.s. & 1 l.s.), A.50/79 (4 t.s. & 1 l.s.), A.50/94 (4 t.s. & 1 l.s.), all specimens from bed 50.

Breviphrentis cf. *superstes*:
- Sivry: S-66B-I (1 t.s. & 1 l.s.), S-66B-II (1 l.s.), S-66B-III (1 t.s. & 1 l.s.), S-66B-IV (2 t.s.).
- Badon: B-1 (1 t.s. & 1 l.s.), B-2 (1 t.s. & 1 l.s.) , B-4 (1 t.s.), B-5 (2 t.s.), B-7 (1 t.s.), B-9 (5 t.s. & 1 l.s.).

Catactotoechus sp.:
- Chevetogne: Chev. 1993/1-I (2 t.s.), Chev. 1993/1-II (2 t.s.).

Cheilaxonia cf. *hofmanni*:
- Lambermont: Lambermont/2011/11/I to V, 2011/12/I to VI, 2011/13/VII to XV, 2011/14/XVI to XXIV, 2011/15/XXV to XXIX, 2011/16/XXX to XXXVII, 2011/17/XXXVIII to LIII, 2011/18/LV to LX (60 t.s. , 5 l.s.).

Neaxon sp.:
- Lambermont: Lambermont 2011/12/I' (1 t.s.), 2011/15/XXVI (1 t.s.).

Amplexus sp.:
- Isnes-les-Dames/dec.2011/I (4 t.s., 1 l.s.).

Tabulophyllum ? sp.:
- Isnes-les-Dames/dec.2011/II (6 t.s.).

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