

# Royseux: a palaeobiodiversity hotspot in the Late Viséan (Carboniferous) of Belgium

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**ABSTRACT.** Biodiversity hotspots are defined as areas of unusually high biological diversity. This definition is less clear for palaeohotspots but the Royseux locality in Southern Belgium is interpreted as such a site because of the large number of coral species that co-occur within a small area and short time interval. Forty-one species (29 genera) of rugose, tabulate and heterocorallia corals are known within a 6 m-thick 4<sup>th</sup> order parasequence (100 kyr). These numbers increase to 50 species in 30 genera if the entire succession is considered. Consequently, Royseux is regarded as the richest site for late Viséan coral diversity on a global scale. Comparison with other sites from Spain, Morocco, the British Isles, and eastern Australia confirms this view. The diversity of brachiopods (at least 18 species within 16 genera) and other invertebrates is also assessed. The great palaeobiodiversity is tentatively explained by the interplay of several global and local causes, including high late Viséan biodiversity at the global scale associated with tectonically and sedimentary-driven micro-environment differentiation. Conversely, the Royseux locality has yielded few endemic taxa.

**KEYWORDS:** biodiversity, disparity, hotspot, endemism, corals, brachiopods, reef, Carboniferous.

## 1. Introduction

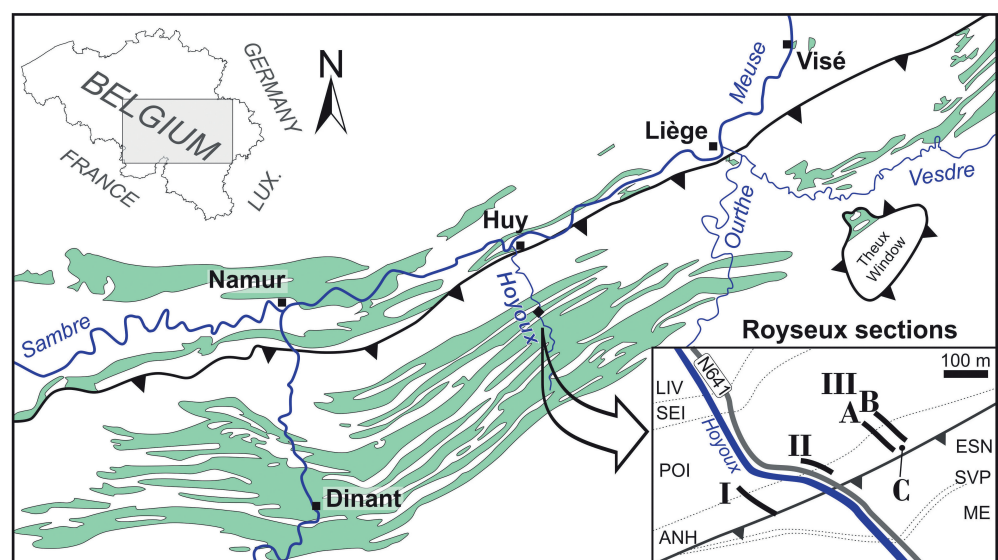
Quantifying biodiversity has become a major concern, not only for modern ecology and nature conservation, but also in the fossil record, where the aim is understanding the effects of global changes on the diversity of past life. During the last decade the palaeontological literature dealing with changes in biodiversity over large time scales (periods, stages) has increased significantly. Unfortunately, most papers failed the difficult task of pinpointing the origin of biodiversity: why so many taxa occur(ed) in a particular area at a particular time, why is the diversity not globally distributed, and why do many taxa occur only in localised areas?

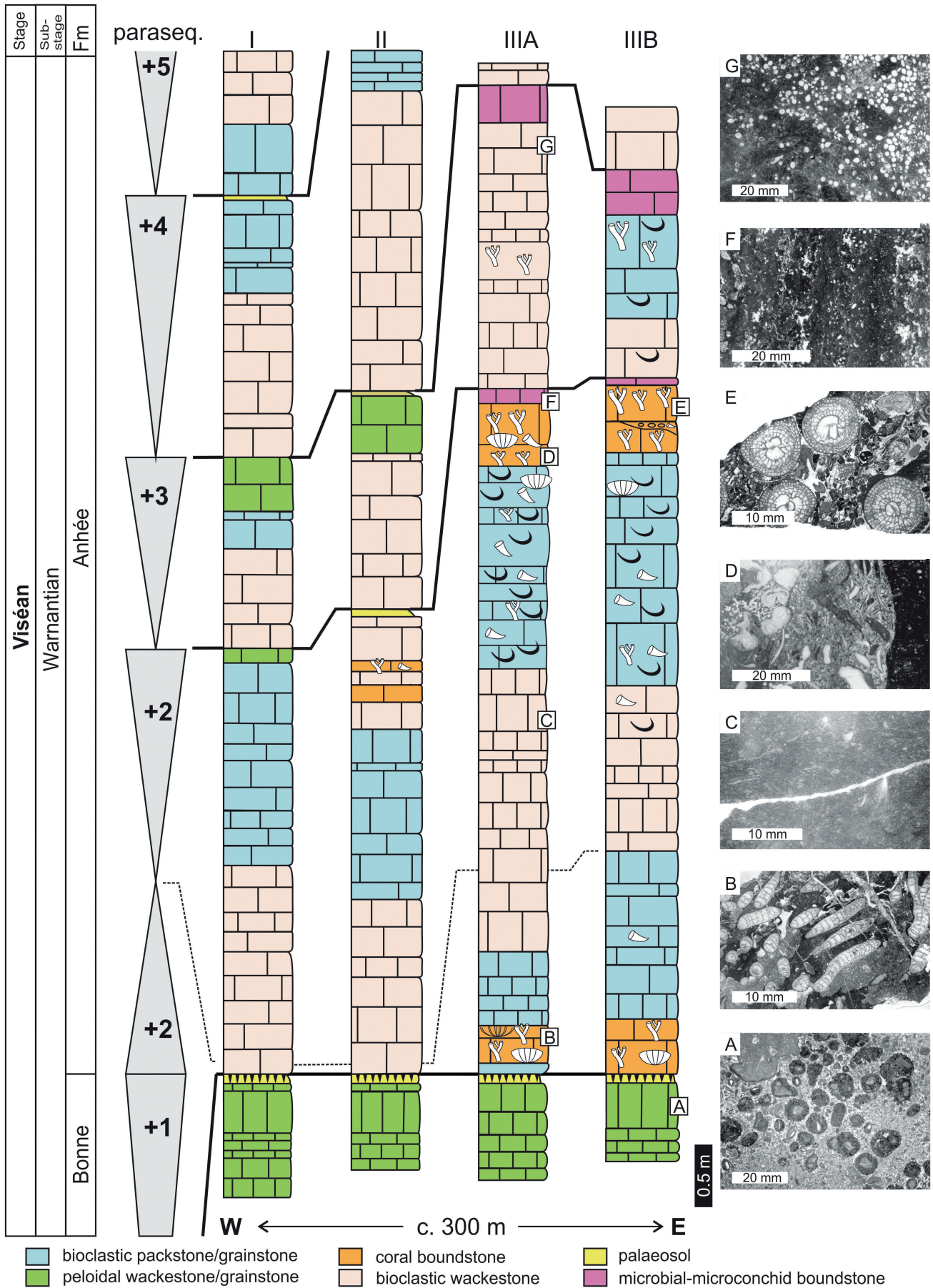
Biodiversity hotspots are sites or areas with an unusually high numbers of co-occurring species (Myers, 1988). Present-day biodiversity hotspots are defined as biogeographic areas where the density of co-occurring species is extraordinarily high (Marchese, 2015) and/or as areas with a high density of endemic species, most of which are currently suffering habitat loss (Myers et al., 2000). Although this definition is easily applicable to present biodiversity, it is difficult to recognise ancient biodiversity hotspots and few examples have been recorded (e.g. origin and shift of modern marine tropical hotspots of the Indo-Australian Archipelago: Renema et al., 2008; mollusc palaeo-hotspot in the Lutetian of the Paris Basin: Merle, 2008;

endemic crinozoan hotspots in the Pennsylvanian of North America: Waters & Webster, 2012). Nevertheless, in the case of fossil assemblages, the time scale enters into the equation because each assemblage represents a certain amount of time. To understand ancient diversity hotspots it is necessary to focus on as narrow a time interval as possible in order to avoid temporal dilution of the signal due to the shift of environments and thus ecosystems through time. The number of taxa (species, genera, etc.), irrespective of their phylogenetic relationship, is commonly used to denote total diversity, but it is strongly biased by the quality of the geological record, taphonomy and sampling effort, and tabulation methods have been abundantly criticised (see discussion in Cecca, 2002; Brown & Lomolino, 2010). Hence, a second condition for a well-defined hotspot is a fossiliferous site characterised by well-preserved fossils, well-established geological context and sampling as comprehensive as possible. However, temporal issue in biodiversity can be circumvented through the use of normalised diversity (standing diversity rather than total diversity, see Webb et al., 1997, for example)

The Royseux locality in southern Belgium (Fig. 1) is such a site. The considered time slice corresponds roughly to a 4<sup>th</sup> order parasequence (100 kyr); its geological and palaeoenvironmental settings are well understood; the preservation is generally excellent; and the faunal record results from more than 40 years of sampling.

**Figure 1.** Locality map of the Royseux sections in the Dinant Synclinorium (green areas represent the Lower Carboniferous outcrop zones) with a close-up view showing the position of sections I, II, IIIA, IIIB and borehole IIIC. Legend: ESN: Esneux Formation (Fm), SVP: Souverain-Pré Fm, ME: Montfort-Evieux Fm (Famennian), LIV: Lives Fm, SEI: Seilles Mbr, POI: Poilvache Mbr (both within Grands-Malades Fm), ANH: Anhée Fm. General map after Poty et al. (2006), geological map after Barchy & Marion (in press) and Mottequin & Marion (in press).

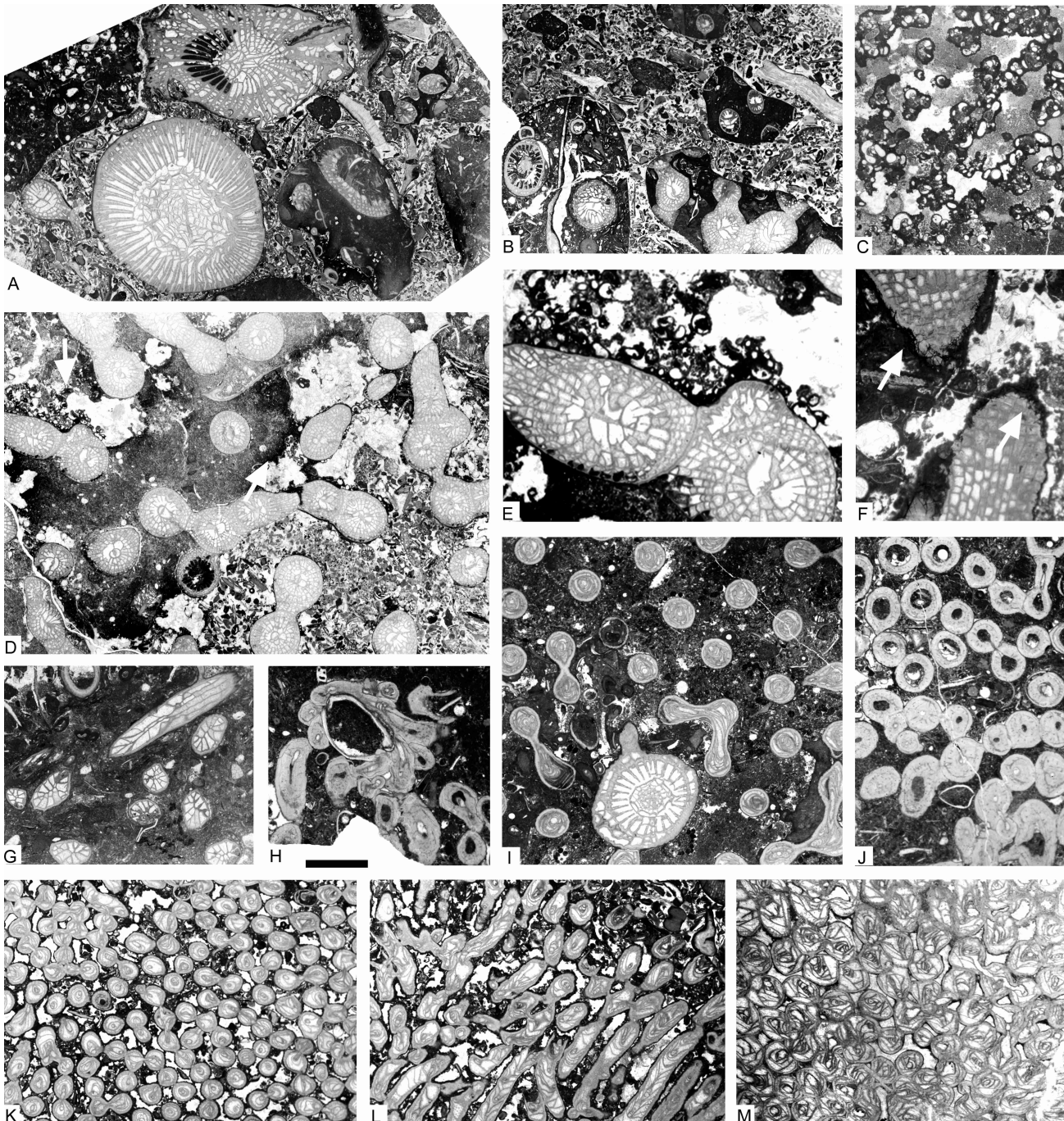




**Figure 2.** Logs of the Royseux sections (I, II, IIIA and IIIB, see Fig. 1 for location) with indication of the parasequences (+1 to +5) and the main facies. A: peloidal packstone-grainstone with centimetric oncoids. B: *Siphonodendron junceum* bafflestone. C: fine-grained bioturbid bioclastic packstone. D: coarse bioclastic rudstone with fragments of gigantoproductid, rugose corals and pelmatozoans. E: *Siphonodendron martini* bafflestone with a bioclastic grainstone matrix. F: microbial-microconchid boundstone. G: *Saccaminopsis* packstone. Modified from Poty et al. (2011).

	global abundance	first biostrome	bioclastic facies of paraseq. +2	gigantiproductions beds of paraseq. +2	second biostrome	conglomerate horizon	complete paraseq. +2	paraseq. +3	upper paraseq. (RC8)
<i>Amygdalophyllum</i> sp.	*					*	*		
<i>Arachnolasma</i> sp.	*						*	*	
<i>Aulophyllum fungites</i>	****				*	***	***	*	**
<i>Axophyllum densum</i>	***		*	*	*	*	*	*	*
<i>Axophyllum lonsdaleiforme</i>	*								*
<i>Axophyllum nanum</i>	****		*	**	*	*	**	*	*
<i>Axophyllum pseudokirsopianum</i>	*					*	*		
<i>Axophyllum</i> sp.	*					*	*		
' <i>Bothrophyllum</i> ' <i>lateseptatum</i>	*					*	*		
<i>Caninophyllum halkynense</i>	**					*	*		
<i>Clisiophyllum crassiseptatum</i>	**					*	*	*	
<i>Dibunophyllum bipartitum</i>	****				*	***	***	**	**
<i>Dibunophyllum</i> sp.	*					*	*		
<i>Diphyphyllum fasciculatum</i>	*				*		*		
<i>Diphyphyllum furcatum</i>	**				*		**		
<i>Diphyphyllum lateseptatum</i>	***			*	**	*	***	*	**
<i>Diphyphyllum maximum</i>	*								*
<i>Enniskilenia enniskileni</i>	**					*	*		*
<i>Gangamophyllum</i> sp.	*					*	*		
<i>Guadatia</i> sp.	*					*	*		
<i>Haplolasma</i> cf. <i>densum</i>	*					*	*		
' <i>Kizilia</i> ' sp.	*					*	*		
<i>Koninckophyllum interruptum</i>	*				*	*	*	*	*
<i>Koninckophyllum magnificum</i>	*				*	*	*	*	
<i>Lithostrotion decipiens</i>	**				*		**		
<i>Lithostrotion maccoyanum</i>	***	***				*	***		*
<i>Lithostrotion vorticale</i>	**				*	*	**		
<i>Lonsdaleia</i> aff. <i>duplicata</i>	**								*
<i>Lonsdaleia</i> sp.	*								*
<i>Palaeosmilia murchisoni</i>	**					*	*		*
<i>Palastraea</i> cf. <i>carbonaria</i>	*								*
<i>Pareymia spendens</i>	**								*
<i>Pseudozaphrentoides juddi</i>	****					***	***	*	*
<i>Rylstonia</i> cf. <i>benecompecta</i>	*					*	*		
<i>Siphonodendron</i> aff. <i>junceum</i>	*								*
<i>Siphonodendron intermedium</i>	***				**	*	***		
<i>Siphonodendron irregulare</i>	*	*					*		*
<i>Siphonodendron junceum</i>	****	***	*	*	**	**	****		*
<i>Siphonodendron martini</i>	****			*	****	*	****	*	*
<i>Siphonodendron pauciradiale</i>	****	*		*	**	**	***	*	***
<i>Siphonophyllia samsonensis</i>	*					*	*		
<i>Siphonophyllia</i> sp.	*								*
total Rugosan species	42	4	3	5	15	29	34	12	22
total Rugosan genera	35	2	2	3	6	18	22	9	13
<i>Heterophyllia ornata</i>	****	*	*	*	*	*	**	*	*
<i>Hexaphyllia mirabilis</i>	***	*	*	*	*	*	**	**	**
<i>Syringopora</i> sp. 1	**	**					*	*	
<i>Syringopora</i> sp. 2	*				*		*		
cladochonid	*				*		*		
chaetetid	**				*	*	*		*
multithecoporid	*			*			*		
roemeriporid	*								**
total coral species	50	7	5	9	20	31	41	15	26
total coral genera	30	5	3	5	11	21	29	11	17

**Table 1.** Distribution and abundance of corals in the dominant facies and units of Royseux. Legend: \*: rare, \*\*: scattered, \*\*\*: common, \*\*\*\*: abundant. From Poty (1981) and Denayer et al. (2011), updated and completed (total: 290 specimens).



**Figure 3.** Facies and corals from the Chabôfosse facies of Royseux. A: limestone conglomerate with reworked pebbles of several distinct facies as well as corals, the solitary coral at the base is *Clisiophyllum crassiseptatum* with perfectly preserved epitheca suggesting that it grew amongst the pebbles very shortly after their deposition (ULg.PA.Roy.III.66b). B: conglomerate with limestone pebbles of reworked fragments of *Siphonodendron* ssp. colonies (ULg.PA.Roy.III.272). C: microconchids associated with microbial-algal build-ups from the uppermost facies of sequence +2 (ULg.PA.Roy.III.271). D: *Siphonodendron intermedium* colony partly included in a pebble (darker facies), partly free suggesting either that the reworking occurred quickly and on short distance or possibly that the survived the reworking and continued to grow afterwards, or a ‘patchy’ diageneses of the matrix (ULg.PA.Roy.I.13a). E: close-up view of D showing microconchids encrusting edges of the pebble and free corallites. F: *Diphyphyllum lateseptatum* reworked in the conglomerate with margin burrowed by endoliths (arrows) suggesting that reworking was short-lived and was followed by a period of relative calm and slow sedimentation (ULg.PA.Roy.III.273). G: *Hexaphyllia ornata* from the upper biostrome of sequence +2 (ULg.PA.Roy.III.120). H: Undetermined cladochond growing on a brachiopod shell (ULg.PA.Roy.III.244b). I: *Axophyllum simplex* settled within a colony of *Syringopora* sp. 1 (ULg.PA.Roy.III.89). J: Undetermined multithecoporid with variously thickened thecae (ULg.PA.Roy.III.244). K-L: *Syringopora* sp. 2 in transverse and longitudinal section (ULg.PA.Roy.III.249). M: *Roemeripora* sp. in transverse section, from sequence +9 (ULg.PA.Roy.I.274). Scale bar equals 10 mm for A, B, D and E and 5 mm for C, F-M.

## 2. Settings

The Royseux locality is situated in the Dinant Synclinorium, a part of the Variscan Complex present in Southern Belgium. During Devonian and early Carboniferous times, the Dinant Synclinorium belonged to a narrow platform stretching along the south coast of the London-Brabant Peninsula (Laurussia) from the Aachen area (westernmost Germany) in the east to the Bristol area (United Kingdom) in the west. The Belgian part of this platform is traditionally named the Namur-Dinant Basin.

This ‘basin’ – in fact a half-graben – was subdivided into several sedimentation areas by Hance et al. (2001).

Royseux is located in the central part of the Namur-Dinant Basin, and thus belongs to the Condros Sedimentation Area (CSA). A thick sequence of shallow-water limestone was deposited in this sedimentation area during Warnantian (late Viséan) time. The Warnantian succession is subdivided in ascending order into the Bonne (Thon-Samson and Poilvache members) and Anhée formations (Poty et al., 2006). The latter includes unusual coral biostromes and coralliferous beds (Aretz, 2001; Fig. 2), which

correspond to the Chabôfosse Facies sensu Poty et al. (2001). Detailed description of the sections is available in Poty et al. (1988, 2011) and Aretz (2001, 2002) and is briefly summarised here. The base of the Anhée Formation (Fm) rests on a palaeosol capping the sequential stromatolitic and oncolitic limestones of the Poilvache Member and corresponds to a shift in sedimentation from deepening-upward to shallowing-upward parasequences (recorded by sequence +2 of Pirlet, 1968). All succeeding sequences follow this trend and start with loosely packed bioclastic wackestone passing to packstone then grainstone to rudstone; the top of the sequences are micritic and microbial wackestones. Bioclasts are mainly fragments of echinoderms, brachiopods, corals, bryozoans and foraminifers. Less common facies include *Saccaminopsis* wackestone, microbial boundstone associated with microconchids ('vermetid gastropods' in older literature) and coral bafflestone (Aretz, 2001). Two coral horizons occur in the succession, at the base and top of parasequence +2. The first horizon (Fig. 2) is a *Siphonodendron junceum* and *Lithostrotion maccoyanum* bafflestone that rests on crinoidal rudstone and is succeeded by a monospecific layer of *S. junceum*. *Siphonodendron pauciradiale*, syringoporids and heterocorals occur at the top of this first biostrome. The middle part of parasequence +2 yields a rich and diverse fauna of colonial (mainly *Siphonodendron* ssp.) and solitary rugose corals (*Dibunophyllum bipartitum*), whereas chaetetids and syringoporides occur sporadically. Brachiopods are abundant and dominated by spiriferides and productives, including representatives of the Subfamily Gigantoproductinae. The second biostromal horizon starts with a *S. junceum* bafflestone with a bioclastic wackestone-packstone matrix, capped by a poorly sorted pebbly rudstone (up to 25 cm-thick) containing well rounded fragments of colonies (*Siphonodendron* ssp., *Diphyphyllum* ssp.) and numerous solitary rugose corals. This conglomerate was interpreted as a storm deposit by Aretz (2001). The diversity is at a maximum in this conglomeratic layer, both for rugose corals (31 species, Table 1) and brachiopods (10 species). The biostrome ends with a *Siphonodendron martini* bed resting on the conglomerate and is capped by a microbial-algal

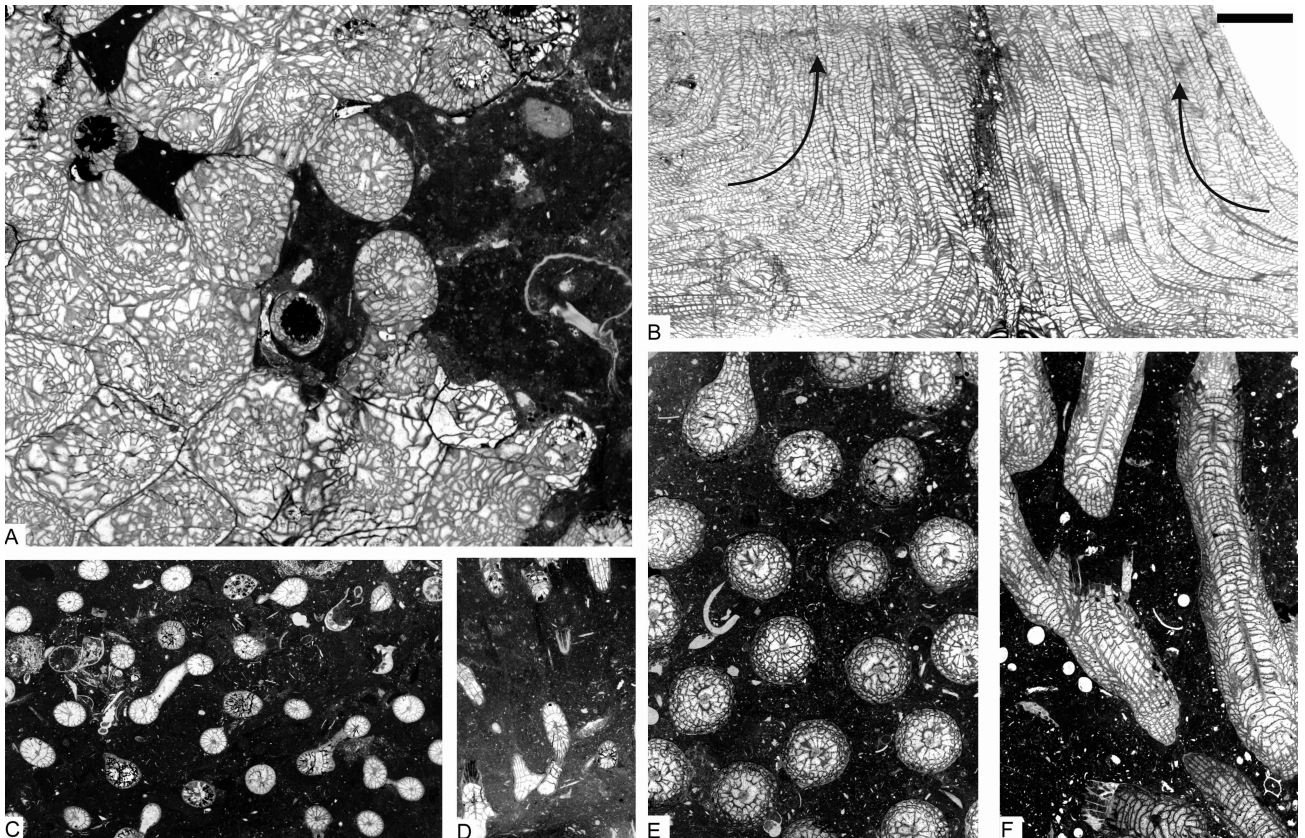
crust associated with microconchids that marks the boundary with the next parasequence. Parasequence +3 starts with bioclastic wackestone-packstone containing some corals and *Saccaminopsis* wackestone and is topped by a horizon formed by small microbial-heterocoral-microconchid build-ups (Fig. 3C). Parasequences +4 to +8 are relatively rich in fauna (Poty et al., 1988) but poorly exposed. The first late Warnantian (Brigantian) fauna appear in parasequence +9 (see Poty et al., 1988).

### 3. Faunal assemblages

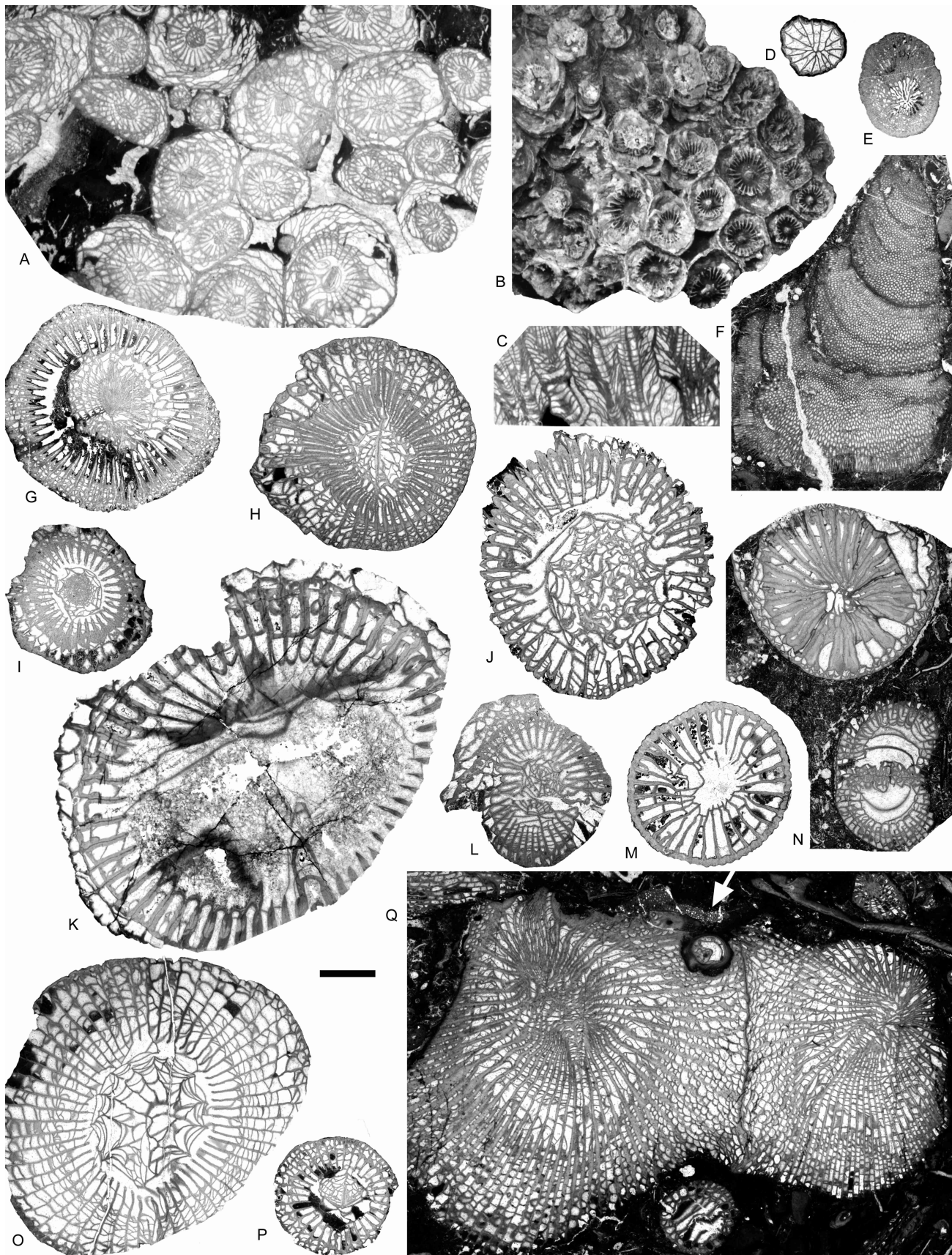
In the stratigraphical interval studied, six lithological units are recognised: five in parasequence +2 (first biostrome, intermediate bioclastic beds, gigantoproductines beds, second biostrome, and conglomerate; see previous section); a further unit consists of the fossiliferous beds immediately overlying the second coral horizon (parasequence +3). These six units are characterised by their fossil assemblage (Table 1). Sampling for groups other than corals (i.e. brachiopods, molluscs, foraminifers) is less precise and assemblages are available for groups of units.

#### 3.1. Rugose corals

The lower coral biostrome (Fig. 2) yields a bi-specific assemblage of *Siphonodendron junceum* and *Lithostrotion maccoyanum* in colonies to 60 cm in diameter. It is classified as a low-medium diversity coral biostrome (class C2 in Aretz, 2010). Very rare *Siphonodendron irregulare* and *S. pauciradiale* occur. Overlying bioclastic strata are relatively poorly fossiliferous and contain a few colonies of *S. junceum* together with the solitary taxa *Axophyllum nanum* and *A. densum*. This unit corresponds to a low diversity level-bottom community (A2 in Aretz, 2010) possibly owing to the development of very shallow-water facies (Aretz et al., 2010). The diversity increases again in the gigantoproductines beds that recorded the next deepening. In addition to the previously listed species, *Siphonodendron martini*, *S. pauciradiale* and *Diphyphyllum* sp. occur in colonies tens of centimetres across (class A1 of Aretz, 2010). The diversity increases rapidly with the



**Figure 4.** Colonial rugose corals from sequence +2 of the Chabôfosse facies of Royseux. A: sub-ceroid colony of *Lithostrotion vorticale* showing sub-cylindrical corallites (ULg.PA.Roy.III.254). B: Two colonies of *Lithostrotion maccoyanum* converging then growing parallel to each other (ULg.PA.Roy.III.252). C-D: *Siphonodendron irregulare* (ULg.PA.Roy.III.175). E-F: *Siphonodendron* aff. *junceum* characterised by very small corallites, 1 mm or less in diameter (ULg.PA.Roy.III.210). Scale bar equals 5 mm for A-F.



**Figure 5.** Rugose corals and chaetetid from the Chabôfosse facies of Royseux. A-C: *Lonsdaleia* sp. from sequence +9 showing a sub-ceroid trend (ULg.PA.Roy.I.217), A: transverse section, B: external view of corallum, C: longitudinal section. D: *Heterophyllia ornata* (ULg.PA.Roy.II.234). E: '*Kizilia*' sp. from sequence +2 (ULg.PA.Roy.III.92). F: cf. *Chaetetes depressus* from sequence +2 (ULg.PA.Roy.III.234/I/i). G: *Amygdalophyllum* sp. 1 (ULg.PA.Roy.III.221/I). H: *Arachnolasma* sp. (ULg.PA.Roy.III.108b). I: *Axophyllum lonsdaleoides* (ULg.PA.Roy.III.178). J: *Gangamophyllum* cf. *boreale* (ULg.PA.Roy.III.173). K: *Siphonophyllia samsonensis* (ULg.PA.Roy.III.223). L: *Axophyllum* sp. 2 (ULg.PA.Roy.III.154/II). M: *Enniskillenienia enniskilleni* from sequence +9 (ULg.PA.Roy.III.142a). N: *Siphonophyllia* sp. (juvenile?) and *Diphyphyllum maximum* (ULg.PA.Roy.III.207a). O: *Dibunophyllum bipartitum* forma '*craigana*' (ULg.PA.Roy.III.155). P: *Dibunophyllum* sp. (ULg.PA.Roy.III.233/II). Q: *Palaestraea* cf. *carbonica* with chaetetid sponges and microconchids (arrow) from sequence +9 (ULg.PA.Roy.III.153). Scale bar equals 10 mm for B and 5 mm for A, C-Q.

development of the second biostrome in which *Siphonodendron martini* (in large colonies) is highly dominant, whereas *S. intermedium*, *S. pauciradiale*, *S. junceum*, *Clisiophyllum crassiseptatum* (Fig. 3A) and *Dibunophyllum bipartitum* are very common. Additionally, scattered *Lithostrotion vorticale*, *L. decipiens*, *Diphyphyllum lateseptatum*, *Aulophyllum fungites*, *Pseudozaphrentoides juddi*, *Axophyllum nanum*, and *Axophyllum densum* are moderately abundant but *Diphyphyllum furcatum*, *D. fasciculatum*, *Koninckophyllum interruptum* and *K. magnificum* are rather rare. The remarkable conglomerate horizon that occurs in the median part of the second biostrome consists of reworked, recently formed limestone including coral colonies. The preservation of corals in the conglomerate is very good, probable evidence of short transport distances. Solitary corals appear either as reworked elements (in pebbles or matrix-free, Fig. 3A-B) and as autochthonous fauna that seemingly grew up in the gravel after its deposition. These corals include *Aulophyllum fungites* and *Dibunophyllum bipartitum* (both abundant, Fig. 4O), *Dibunophyllum* sp. (rare, Fig. 4P), *Palaeosmia murchisoni*, *Caninophyllum halkynense* (both common), ‘*Botrophyllum*’ *lateseptatum* (rare), *Koninckophyllum magnificum* (rare), *K. interruptum*, *Siphonophyllia samsonensis* (very rare, Fig. 4K), *Pseudozaphrentoides juddi* (very common), *Haplolasma* cf. *densum*, *Gangamophyllum densitabulata* (rare, Fig. 4J), *Axophyllum nanum* (common), *A. densum*, *A. pseudokirsopianum* (rare), *A. sp.* (rare, Fig. 3L), *Rylstonia* cf. *benecompecta* (rare), *Guadatia* sp. (rare), *Amygdalophyllum* sp. (Fig. 4G), ‘*Kizilia*’ sp. (very rare, Fig. 4E) and *Enniskillenia enniskilleni* (occasional, Fig. 4M). The overlying strata of parasequence +3 yield a less diversified fauna dominated by *Siphonodendron martini*, *S. pauciradiale*, *Diphyphyllum fasciculiseptatum*, *Aulophyllum fungites* and *Dibunophyllum bipartitum*, together with *Clisiophyllum crassiseptatum*, *Arachnolasma* sp. (Fig. 4H), *Pseudozaphrentoides juddi*, *Axophyllum nanum* and *A. densum*. Each species is known from older strata. A supplementary, younger unit (parasequences +8/9, RC8 biozone of Poty et al., 2006) is described here also because of its relatively high diversity. *Siphonodendron pauciradiale* is highly dominant, but *S. martini*, *S. junceum*, *S. aff. junceum* (a species with very small diameter corallites, Fig. 5C-D), *Lithostrotion maccoyanum* (Fig. 5B), *Diphyphyllum lateseptatum*, *D. maximum*, *Aulophyllum fungites*, *Dibunophyllum bipartitum*, *Koninckophyllum interruptum*, *Siphonophyllia* sp. (Fig. 4N), *Pseudozaphrentoides juddi*, *Palaeosmia murchisoni*, *Axophyllum nanum*, *A. densum*, *A. lonsdaleiforme* (Fig. 3I), *Lonsdaleia duplicata* and an as yet undescribed *Lonsdaleia* species (Fig. 4A-C), *Palaestraea* cf. *carbonaria* (Fig. 4Q), *Pareynia splendens* and *Enniskillenia enniskilleni* are common in several beds.

### 3.2. Tabulate corals

Curiously, tabulate corals are rather uncommon in the locality, possibly for reasons of facies issues and/or competition with rugose corals (particularly with *Siphonodendron junceum*). *Syringopora* sp. 1 (Fig. 3I) is common only in the lower part of the first biostrome. *Syringopora* sp. 2 (with smaller corallites than *S. sp. 1*, Fig. 3K-L) occurs scattered in the second biostrome and parasequence +9. Cladochonids occur sporadically in the second biostrome and its conglomerate (Fig. 3H), whereas a single occurrence of multithecoporids (Fig. 3J) occurs in the gigantoproductine beds of parasequence +2. Roemeriporids (Fig. 3M) are known only in parasequence +9.

### 3.3. Heterocorals

*Heterophyllia ornata* and *Hexaphyllia mirabilis* are relatively common and occur in all the units but are particularly abundant in the small microbial build-ups of unit +4 (Fig. 3G, 5D).

### 3.4. Sponges

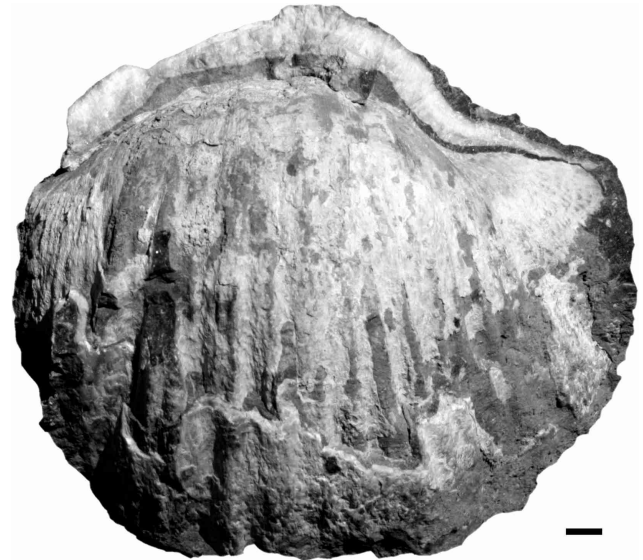
Chaetetids are scattered in the second biostrome and in the conglomerate, invariably as small colonies (Fig. 5F). Siliceous sponge spicules were observed in various units but none have been studied systematically.

### 3.5. Microfossils

Conodont, algal and foraminiferal assemblages were investigated in a MSc thesis (Laurent, 1985) in collaboration with R. Conil and M. Laloux. No exhaustive lists are available for the individual groups, but Laloux (1988) qualified the diversity of the foraminifers of Royseux as one of the highest ever recorded in the Namur-Dinant Basin.

### 3.6. Brachiopods

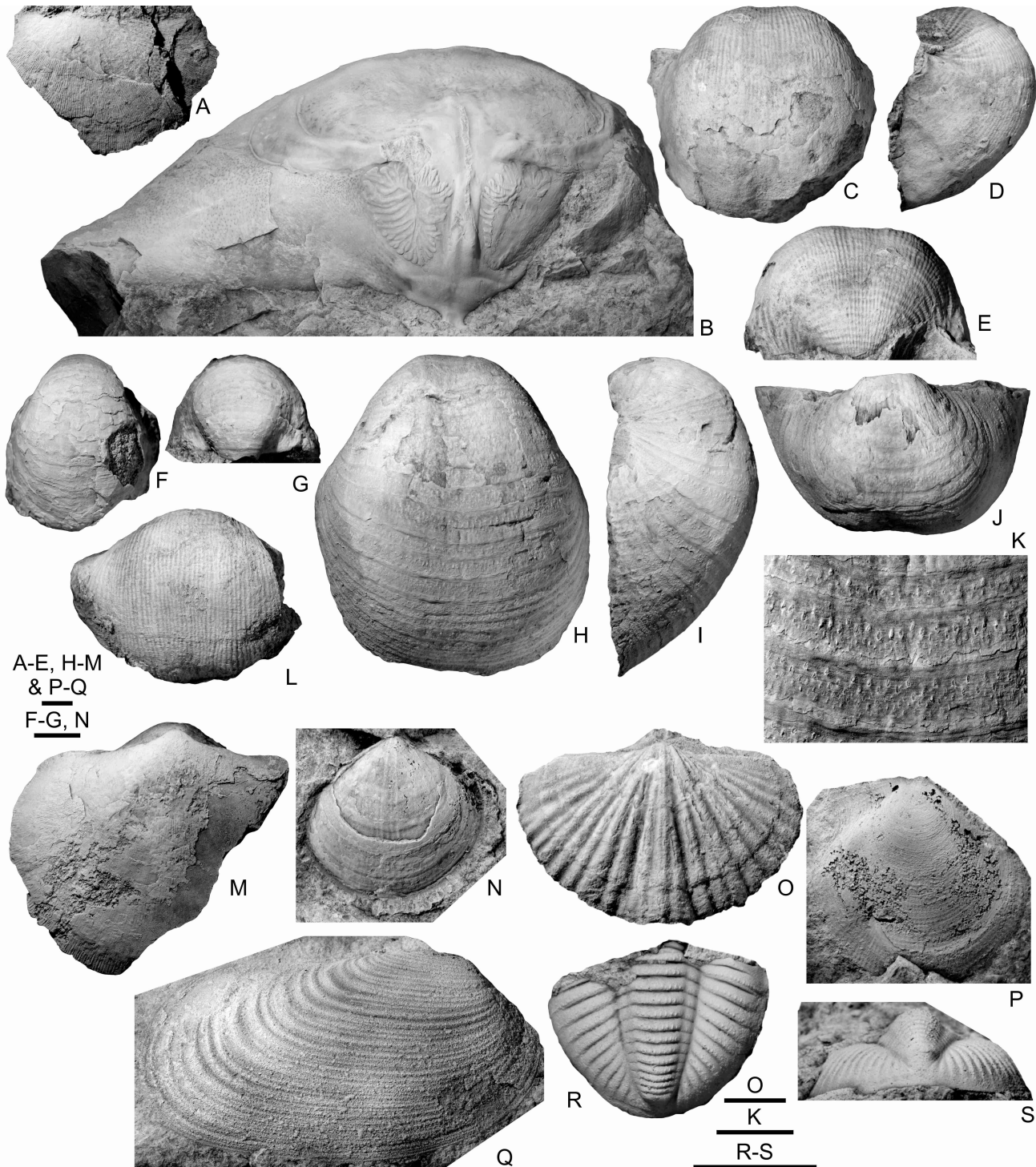
The Royseux brachiopod (at least 18 species) contains some remarkable horizons rich in large-sized productidines (*Gigantoproductus giganteus*, Figs 6, 7B). This is so far the best



**Figure 6.** *Gigantoproductus giganteus*, ULg.PA.2015.08.01/1, incomplete large-sized specimen (mostly the dorsal external mould) with shelly fragments of dorsal and ventral valves. Note the thick ventral valve and the strong longitudinal plications. Scale bar equals 10 mm.

locality in Belgium to observe them in situ even if representatives of the Subfamily Gigantoproductinae were reported, but not illustrated (except de Koninck, 1847), elsewhere in the Namur-Dinant Basin (see e.g. references in Mortelmans & Bourguignon, 1954; Demanet, 1958). Besides this emblematic species, the brachiopod fauna includes chonetidines (*Megachonetes* sp., Fig. 7A), other productidines (*Antiquatonia* sp., Fig. 7C-E), *Avonia* sp. (Fig. 7F-G), *Echinoconchus punctatus* (Fig. 7H-K), *Echinoconchella* sp., *Semiplanini* gen. et sp. indet. (Fig. 7L), productide gen. et sp. indet., unidentified orthotetides, orthides (*Schizophoria resupinata*, Fig. 7M), rhynchonellides (*Propriopugnus?* sp.), athyridines (*Actinoconchus* sp., Fig. 7N), spiriferides (*Podtsheremia* ssp., possibly two species) (Fig. 7O), elythid gen. et sp. indet., spiriferide (two undetermined genera and species), and undetermined terebratulides. These data should be considered as preliminary pending on thorough systematic study of additional material collected from each horizon (some species are represented by only a single specimen whereas the gigantoproductines are over-represented); hence, most brachiopods are here left in open nomenclature. Parasequence +2 yields some unidentified orthotetides, *Schizophoria resupinata*, *Podtsheremia* sp., spiriferide gen. et sp. indet. 1. The second biostrome yields *Antiquatonia* sp., *Avonia* sp., *G. giganteus*, *Podtsheremia* sp., spiriferide gen. et sp. Indet 2. The conglomerate contains *Antiquatonia* sp., *Avonia* sp., *Schizophoria* gr. *resupinata*, *G. giganteus*, *Semiplanini* gen. et sp. indet., *Echinoconchus punctatus*, orthotetide gen. et sp. indet., *Propriopugnus?* sp. The overlying strata (parasequence +3) yield *Echinoconchus punctatus* and productide gen. et sp. indet. and other undetermined taxa.

The degree of articulation of the shells and the state of preservation of delicate ornamental elements (e.g. spines, frills) rank among the most significant factors for establishing the assemblage type (Brunton, 1987). Nevertheless, it is difficult to



**Figure 7.** Brachiopods, trilobites and molluscs from the Chabôfosse facies of Royseux. A. *Megachonetes* sp., ULg.PA.2015.08.01/2, incomplete specimen in ventral view. B. *Gigantoproductus giganteus*, ULg.PA.2015.08.01/3, incomplete dorsal interior in posterior view (note the dendritic adductor muscle scars). C-E. *Antiquatonia* sp., ULg.PA.2015.08.01/4, almost complete ventral valve in ventral, lateral and posterior views. F-G. *Avonia* sp., ULg.PA.2015.08.01/5, incomplete ventral valve in ventral and posterior views. H-K. *Echinoconchus punctatus*, ULg.PA.2015.08.01/6, slightly distorted specimen in ventral, lateral and posterior views, and close-up of spines in central part of ventral valve. L. *Semiplanini* gen. et sp. indet., ULg.PA.2015.08.01/13, incomplete ventral valve. M. *Schizophoria resupinata*, ULg.PA.2015.08.01/7, incomplete specimen in ventral view. N. *Actinoconchus* sp., ULg.PA.2015.08.01/8, dorsal valve with fragment of flanges. O. *Podtsheremia* sp., ULg.PA.2015.08.01/9, complete specimen in dorsal view. P. *Limipecten* sp., ULg.PA.2015.08.01/10. Q. *Allorisma* cf. *sulcata*, ULg.PA.2015.08.01/11. R-S. Unidentified trilobite gen. and sp., ULg.PA.2015.08.01/12, pygidium. Scale bars equals 5 mm.

estimate the proportion of disarticulated specimens versus those with conjoined valves owing to the difficulty of extracting the brachiopods from the carbonate matrix, but many specimens are still articulated, especially among the spiriferides and the productidines. *Actinoconchus* sp. (only one specimen!) shows fragments of nonspinose flanges and some rare specimens (*Antiquatonia* sp.) show ventral halteroid spines reaching 1.5 mm in diameter and c. 20 mm in length. Their length is considerably less than those recorded in some productidines from the Viséan Mognée Formation (Delépine, 1928, e.g. plate 1, figures 1-4;

Mottequin et al., 2015a, figure 13A), which was interpreted as being preserved in a relatively low energy environment with turbiditic sedimentation. As explained by Muir-Wood & Cooper (1960) for representatives of the genus *Antiquatonia* characterised by long trail, it is supposed that the posterior part of the shell was partly buried in carbonate mud with the trail protruding, and thus the hinge and ear spines served to anchor the shell. In contrast, representatives of the Subfamily Gigantoproductinae were devoid of such long hinge spines, but these very large-sized shells, with shelly thickening in their posterior part, were characterised by a



locality	number of specimens	number of species	number of genera	thickness	approximate area	authors	Margalev d	Simpson D	Shanon-Wiener H	Pielou E
Royseux	270	47	24	c. 25 m	10 <sup>2</sup> m <sup>2</sup>	this paper	8.217	0.945	3.293	0.855
Royseux only seq. +2	230	32	21	6 m	5 m <sup>2</sup>	this paper	5.701			
Tiouinine	c. 200	(36?) 30	(26?) 20	c. 50 m	10 <sup>3</sup> m <sup>2</sup>	Rodriguez et al. 2012	5.473			
Tiouinine	c. 200	26	15	c. 50 m	10 <sup>3</sup> m <sup>2</sup>	Said et al. 2013	4.718			
Adarouch	c. 300	28	19	>150 m	10 <sup>3</sup> m <sup>2</sup>	Said et al. 2011	4.734	Data not available		
Tabainout	270	26	19	c. 100 m	10 <sup>3</sup> m <sup>2</sup>	Said et al. 2013	4.466			
El Collado	?	26	16			Rodriguez et al. (in press)				
Little Asby Scar	c. 100	14	9	c. 30 m	10 m <sup>2</sup>	Aretz & Nudds 2005	2.823			
Lion Creek	260	24	19	>100 m	10 <sup>3</sup> m <sup>2</sup>	Webb 1990	4.341	0.996	2.695	0.848

**Table 2.** Comparison of Royseux to other late Viséan fossiliferous sites based on rugose corals diversity and statistics.

thick and prominent ventral umbo that lay in the soft sediment with the long trail extending obliquely upward according to Muir-Wood & Cooper (1960). Some of the large-sized *G. giganteus* at Royseux were preserved in life position.

### 3.7. Molluscs

Bivalves are rare throughout the succession. However, some specimens can be attributed to *Limipecten* sp. and *Allorisma* cf. *sulcata* (Figs 7P-Q). Microconchids (previously interpreted as vermetid gastropods) are locally abundant and form small build-ups with microbialites, especially on top of sequences +2 and +4. Scattered turreted and discoidal gastropods occur but have not been studied. Cephalopods are represented by rare orthoconic nautiloids.

### 3.8. Arthropods

Ostracodes and trilobites are common as fragments in thin sections from all facies and units. However, M. Bless determined some ostracode specimens for Laurent's MSc thesis in 1985, recognising Bairdiacea, Paraparchitacea and Shemonaellids. Trilobites may be abundant in the section but have not been studied in detail (Fig. 7R-S).

### 3.9. Bryozoans

Fragments of Cryptostomata, Fenestrata and Cystoporata occur scattered in thin sections but their diversity is still not estimated.

## 4. Statistics

Diversity metrics such as species diversity or various indices are in some studies regarded as convenient criteria to identify hotspots but should be interpreted more as windows into spatial diversity patterns that are not easy to quantify, even in living examples (Marchese, 2015).

The most commonly used proxy for palaeodiversity estimation is species richness, equivalent to Whittaker's (1972)  $\alpha$ -diversity, which corresponds to the total number of taxa (here total number of species or genera). This is the easiest index to calculate but it is not very useful for comparison between sites. Margalev's index  $d = (S-1)/\ln N$ , where  $S$  is the total number of species (=  $\alpha$ -diversity) and  $N$  the total number of specimens provides a better idea of the diversity as it takes into account the size of the collection. However the index is sensitive to species represented by small numbers of specimens. The Shanon-Wiener, Simpson and Chao indexes are better proxies but one must require the number of specimens recorded for each species and these data are rarely available in the literature. However, they are provided here in Table 2 for the Royseux locality and some other sites.

The rarefaction curve (Fig. 8C) computed for corals is asymptotic showing that the sampling is representative of the

diversity because a larger sample would not significantly increase the diversity. The same curve computed for brachiopods indicates that the sampling is not comprehensive and that higher diversity is expected in a larger sample. Moreover, the stratigraphic distribution differs for corals and brachiopods. Obviously, the corals are more abundant in the biostromes, but both groups are most diverse within the conglomeratic level, suggesting mixing (see next section).

Coral occurrences in the six lithological units are summarized in Table 1. Figure 8 indicates the proportion of each genus in the sample and shows that colonial rugose corals and dissepimented solitary corals with axial structure account for c. 40% each, whereas non-columellate dissepimented solitary corals constitute less than 15%. The remaining 5% corresponds to *Enniskillenia enniskilleni*, the only undissepimented corals known in the Royseux section. The coral disparity is therefore rather low with few morpho-groups sizes which individually show little range of size (massive colonies with/without columella, fasciculate colonies with/without columella, dissepimented solitaires with/without axial structure, undissepimented solitaires).

The high abundance of colonial and columellate solitary corals possibly reflects facies dominance as discussed below.

## 5. Comparison

### 5.1. Rugose coral fauna

The Royseux coral assemblage has high biodiversity, one of the highest in the Viséan (see below). But potentially how high could the diversity be? The statistical data discussed in the previous section provide some insight. However, a comparison with other Late Viséan localities exhibiting 'high diversity' gives a different perspective.

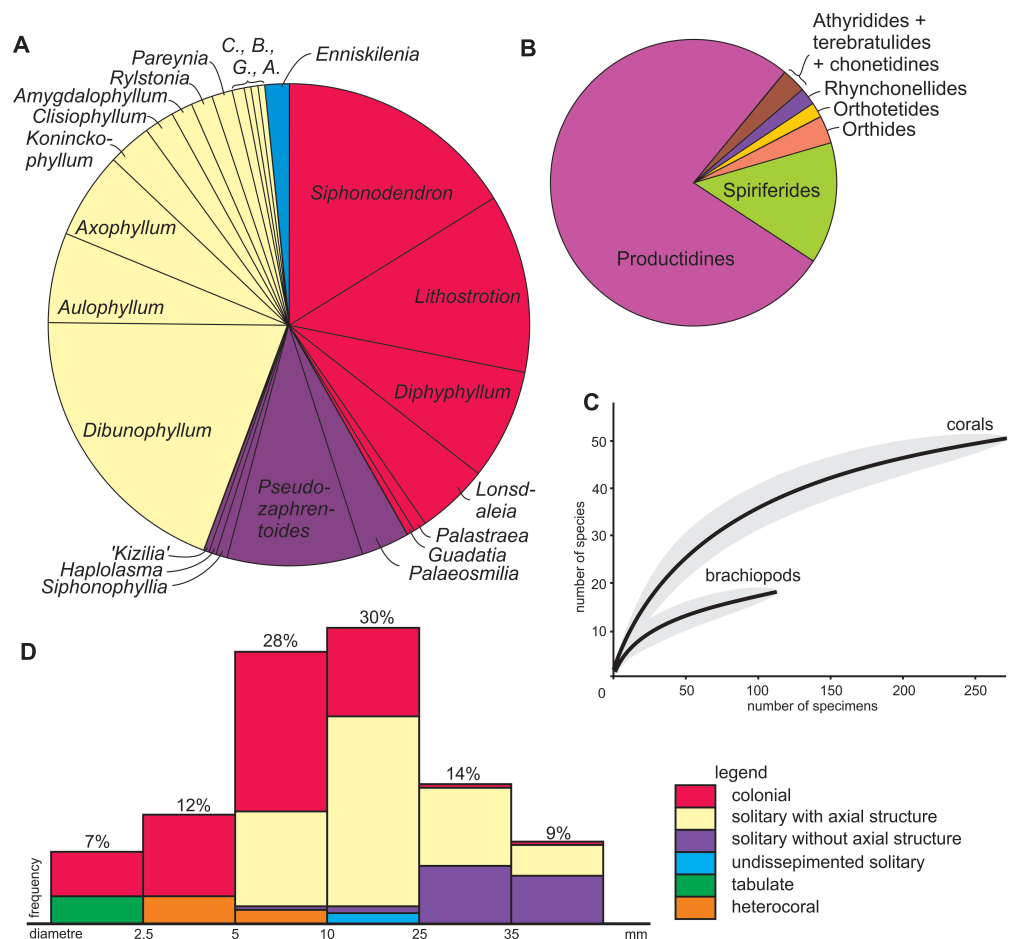
The Visé locality, time-equivalent of the sections at Royseux, is situated within the same biogeographic area as during the late Viséan and has reef facies with a very diverse fauna of brachiopods and molluscs (e.g. gastropods, bivalves, Demanet, 1958 and references within), but interestingly, the rugose and tabulate corals are not particularly diverse (36 species distributed among 23 genera after Poty, 1981). Nevertheless, the amount of described material is not very great, the locality is no longer accessible for additional sampling and is, in general, poorly known (Poty, 1981).

The c. 30 m-thick section at Little Asby Scar (Asbian) in Northern England yields 14 coral species distributed among nine genera and time-equivalent *Siphonodendron* biostromes cropping out in various localities in Ireland have much lower diversity with only 14 species distributed among 11 genera, mostly dominated by colonial forms (Aretz et al., 2010).

**Figure 8.** Diversity statistics.

A: Proportions of rugose coral genera within the Royseux assemblage (based on 290 specimens in thin section) showing the co-dominance of colonial forms and solitary corals with an axial structure and the minor occurrence of undissepimented solitary corals. B: Proportions of brachiopod groups in the site, showing the dominance of the productidines, notably the gigantoproductines and associated forms. C: Rarefaction curves with 95% confidence-interval (grey areas) computed for corals and brachiopods showing that the sampling is far from complete for brachiopods but relatively comprehensive for corals. D: Frequency diagram of coral morpho-groups plotted against their diameter. Abbreviations:

A.: *Arachnolasma*,  
B.: *Bothrophyllum*,  
C.: *Caninophyllum*,  
G.: *Gangamophyllum*.



The coral fauna of the late Viséan of Southern Spain (Guadatio area) was recently summarized by Rodríguez et al. (2016). These authors indicate 62 coral species distributed among 34 genera for the entire area (19 sections) and for the entire late Viséan. The richest section (El Collado) yielded 26 species distributed among 16 genera but corresponds to a time of accumulation of c. 5 Myr.

The late Viséan Lion Creek microbial-coral reefs of the Rockhampton Group in Queensland (Eastern Australia) yields 26 coral species distributed among 12 genera, of which nine species are undissepimented solitary rugose corals known only from microbial habitats (Webb, 1990). This diversity represents material from several reefs and peri-reefal facies scattered over a wide area.

Many localities in Morocco have yielded late Viséan rugose corals but only three of them are discussed here because of their high biodiversity. Rodríguez et al. (2012) indicated the occurrence of 36 coral species in 23 genera in according to the main text, but only 30 species in 20 genera are listed their table 1, from the three c. 50 m-thick Tiouinine sections, which include biohermal, peri-reefal and shaly facies of late Viséan age. Said et al. (2013) worked on the same material and listed only 26 species distributed among 23 genera (20 shown in the table) and 15 genera. Taking into account the larger variation in facies and the doubled thickness compared to Royseux, the Tiouinine locality is not so diverse, even considering the largest reported numbers, which need to be checked. Similarly, the Adarouch sections (Said et al., 2011) yielded 28 coral species (19 genera) from more than 150 m of section, including a wide spectrum of facies and ages (Viséan to Bashkirian). The Tabainout area yields 26 coral species (including six undissepimented solitary forms) in 19 genera (six undissepimented) from c. 100 m of section of various facies. In conclusion, the Moroccan localities owe their diversity to accumulation of taxa over longer time intervals that in fact dilute the diversity signals, which falsely increase because the larger variation in facies seems to enhance the diversity and disparity of corals.

Compared to the other localities, sequence +2 of Royseux, 6 m-thick in total, yielded 32 species (21 genera) of rugose corals,

which makes it the most diverse hotspot for the Late Viséan (and possibly for the whole Carboniferous) rugose corals worldwide (see Table 2 for a comparison). Finally, what is so special about Royseux? Corals are certainly diverse (and abundant) but do the other fossil groups develop a similar diversity and what can they add to the discussion?

During the late Viséan, the Namur-Dinant Basin was situated c. 10°S (Stampfli & Borel, 2002). This is a similar latitudinal position present day Borneo, in the Indo-Pacific Coral Triangle, where coral biodiversity reaches its maximum (more than 700 species in 17 families of scleractinians, Hughes et al., 2013; Johnson et al., 2015). Of course the 700 species occur in a wide area of several thousands of square kilometres, but diversity does not decrease in a linear way when area decreases. Compared to the Recent, the coral diversity that would be expected in Royseux (a few hundreds of square metres) would be higher. For comparison, Heron Reef in the Australian Great Barrier Reef (c. 23 km<sup>2</sup> without lagoon) yielded 120 coral species (Plaisance et al., 2011). However, a key point to consider is that fossil species and genera are based purely on morphology. Comparing fossil morpho-species of rugose and tabulate corals with biological species of extant scleractinian corals consequently is not easy, and mostly results in generally lower numbers of taxa for Palaeozoic coral assemblages.

### 5.2. Brachiopod fauna

At first view, the brachiopod diversity (at least 18 species, Fig. 8B) recorded at Royseux is not exceptional compared to those reported elsewhere in the Viséan of Western Europe, notably by Brunton (1987; 56 species) and Brunton & Tilsley (1991; 125 species) in the Asbian of County Fermanagh (Northern Ireland) and Treack Cliff (Derbyshire), respectively. The degree of diversity is similar to that reported in the late Asbian Meenymore Formation (14 species) of northwest Ireland (Mottequin et al., 2015b), wherein 14 species were interpreted to be an in situ, but time-averaged accumulation. However, the brachiopods from Royseux all occur within a single 4<sup>th</sup> order parasequence in comparison with the much longer time interval represented by

Treak Cliff. The brachiopod fauna from some levels of the Zrigat Formation in eastern Tafilalt (Morocco), although probably underestimated, is quite similar to that of Royseux with 15 species, mainly including productides (e.g. *Gigantoproductinae*) and spiriferides (Mottequin et al., 2016). They are associated with a rich coral fauna, which is still only partly known (Aretz et al., 2013). It is currently difficult to compare and estimate the real diversity of the contemporaneous brachiopod fauna from Visé, which was described in the pioneering works of de Koninck (1842-1844, 1847, 1887) and Demanet (1934). These authors described several tens of species, but also erroneously included Frasnian material, such as '*Hypothyridina cuboides*' (see de Koninck, 1842-1844) and *Spirifer capillaris* (see de Koninck, 1887). So far, only a small number of these many species has been revised (e.g. Muir-Wood & Cooper, 1960; Brunton et al., 1994). Demanet (1958) recorded 26 species in the former 'V3b' unit of the Yvoir area (Dinant sedimentation area), i.e. the Thon-Samson, Poilvache and Anhée formations, but the time interval considered by Demanet (1958) is not comparable with the parasequence sampled at Royseux and Demanet's (1958) list of brachiopods has to be revised, but this is beyond the scope of this paper. It is worth noting that the brachiopod sampling is far from exhaustive compared to the corals as indicated by the rarefaction curve (Fig. 8C). A comprehensive study would require additional material.

## 6. Discussion

### 6.1. Coral assemblage

As commonly observed in biostromal units, one characteristic of the coral fauna in Royseux is the dominant position of the colonial corals, here mainly *Siphonodendron* and *Lithostrotion* in the lower part, and of *Diphyphyllum* in the upper part of the sections (Aretz, 2001). Tabulate corals are not diverse and no species with large corallites are known from any facies (Fig. 8D). In the non-biostromal facies, solitary rugose corals dominate and show several striking features, as outlined below.

(1) The non-dissepimented taxa – the so-called *Cyathaxonia* fauna *sensu* Hill (1981) – are almost absent (Fig. 8A). *Enniskillenia enniskilleni* is the only recorded member and it is moreover a large-sized solitary taxon (see next point). These taxa are commonly found in shaly facies, but they are not restricted to deep-water settings as commonly suggested (e.g. Hill, 1981; Oliver, 1992) and are quite common in environments that were stressful for other corals, such as dysphotic, dysaerobic, cold-water, hyperhaline (?) and turbid environments. Obviously none of those environments are known in Royseux. However, small solitary undissepimented corals are not uncommon in microbialite facies (e.g. Webb, 1987; Mundy, 1994). Such facies occur in the capping beds of the *Siphonodendron* biostromes but no rugose corals are associated with them. Curiously, the undissepimented corals are replaced in that facies by heterocorals! Competitive displacement by heterocorals is a possible explanation for this absence but different ecological requirements might also explain the dominance of heterocorals. Similarly, the simple rugose coral *Amplexus coralloides*, which is rather common in all environments in the Carboniferous is unknown in Royseux, possibly for similar reasons.

(2) The caninimorphic corals are poorly represented in the assemblage, both in number of species and in specimens, with *Pseudozaphrentoides juddi* and *Siphonophyllia* sp. being the only members of the morphotype (Fig. 8A, D). These forms are usually regarded as possible 'mud-stickers' (Hubbard, 1970; Aretz et al., 2010) and the absence of mud in Royseux may explain their rarity. The lack of an axial structure may have been tentatively interpreted as unfavourable for these corals, considering the numerous axophyllids, elisiophyllids, amygdalophyllids and *Dibunophyllum* that proliferated in Royseux.

(3) The typical range of corallum diameter of the solitary corals, all taxa considered, is relatively narrow (see Fig. 8D), as c. 60% of the collection has diameters ranging between 5 and 25 mm. This distribution seems to indicate that the size optimum is linked to environment rather than taxonomy (cf. Hubbard, 1966). However, neither small ('*Kizilia*' sp.) nor very large (*Siphonophyllia samsonensis*) corals are common in any facies.

Among the solitary taxa with no axial structure, the 25-35 mm diameter range is largely dominated by *Pseudozaphrentoides julii*, whereas *Palaeosmilia murchisoni* is one of the only taxa with diameters greater than to 35 mm (the largest specimen is 70 mm wide). The solitary rugose corals with an axial structure have diameters dominantly between 10 and 25 mm but larger specimens of the same taxa (mainly *Aulophyllum fungites*, *Dibunophyllum bipartitum* and *Caninophyllum halkynense*) also occur. Hence, the disparity of the solitary rugose corals is much reduced. For the whole coral assemblage, the disparity is not high either and can be roughly but confidently approached by the number of high taxonomic categories (Ciampaglio, 2002): 8 families belonging to 6 suborders of rugose corals. The disparity (amount of morphological differences among taxa; Erwin, 1994) results from a series of constraints. The latter falls into two broad categories (Gould, 1988, 1989; Erwin, 1994): internal constraints (functional, structural, developmental, genetic, historical) and external constraints (environmental, ecological). The internal constraints are characters that do not interact directly with the physical world and results of developmental process (i.e. septal arrangement, fossula, axial structure). The external constraints corresponds to the characters that permit the taxa to withstand in its environment and ecosystem (i.e. skeletal habitus and thickening, size, septal length, etc.). Although both categories are not easily recognised, Erwin (2007) demonstrated that external constraints are the dominant factor determining morpho-space width, and thus that the disparity is ecologically-driven. In the present example, a low disparity would be interpreted as a low ecological constraint.

(4) Endemism is very low with only three taxa known only from Royseux (*Siphonodendron* aff. *junceum*, '*Bothrophyllum*' *lateseptatum* and an undescribed new species of *Lonsdaleia*). There are no endemic genera. However, the faunal assemblage includes species that have been described from only one other area (e.g. *Guadatia*, only known from Southern Spain). Species in open nomenclature are not considered here because they are not sufficiently known (reduced material available). However, taxic diversity and endemism are commonly decoupled. Centres of endemism mostly occur on the periphery of hotspots (Reaka & Lombardi, 2011; Reaka et al., 2008). This would be consistent with hotspot diversity resulting from the accumulation of taxa through time (Bellwood et al., 2012).

### 6.2. Origin of biodiversity

Biodiversity is a complex phenomenon controlled by various interplaying processes that have been and still are abundantly discussed. Several examples have been described in the literature, such as scleractinian diversity controlled in the recent oceans by tectonics (Wilson & Rosen, 1998; Williams & Duda, 2008; Bellwood et al., 2012), eustacy (Potts, 1983; Fulthorpe & Schlanger, 1989), oceanic circulation pattern (Rosen, 1988; Veron, 2000), climate (Cowman et al., 2013; Bowen et al., 2013) and geological history of taxa (cf. Rosen, 1988, and references within). As summarized by Veron (2000), the diversity and biogeography of Recent scleractinian corals result from the superimposition of three patterns: (1) the diversity at the family level mostly reflects the geological history (climate and sea-level change, landmasses positions, extinction events) that occurred through the Cenozoic; (2) the diversity at the genus level results from the evolution of taxa settled in various biogeographic units; (3) the species diversity is the outcome of the oceanic circulation pattern during the last c. 5 Myr. At a finer scale (e.g. organism communities), the diversity is driven by a complex combination of resources availability, specialists/generalists coexistence, environmental variability and colonisation events as well as functional versatility of the organisms (Bellwood et al., 2006). Diversity is consequently produced by time-specific physical parameters (temperature, currents, landmasses position) but is also partly inherited from previous configurations (Veron, 2000; Karlson et al., 2004; Kiessling, 2009; Kiessling & Kocsis, 2015).

If Royseux can be regarded as a biodiversity palaeo-hotspot – at least for the coral fauna – the question of the cause of this diversity remains open. Several hypotheses are tested here and discussed but none of them by itself is satisfactory and the best

explanation probably rests in a combination of the different factors

(1) Facies. Several distinct facies co-occur in Royseux, from biostromal bafflestone to microbial-microconchid build-ups and limestone conglomerate. Several distinct micro-environments are therefore preserved and their faunal associations are quite distinct. Lateral facies variations are rather abrupt (see descriptions of the sections), but the fossiliferous facies occurs only in a much reduced area (a few hundred metres). This situation is uncommon in Viséan biostromes (cf. Aretz, 2010; Aretz et al., 2010) where facies are rather homogenous, but it is commonly observed in other types of reefs throughout geological history and, of course, in Recent reefs. A part of the biodiversity should be linked with the co-occurrence of micro-environments, but only a small number of facies yields corals at Royseux (Fig. 2): the *Siphonodendron* and *Lithostrotion* bafflestone, the bioclastic floatstone-rudstone (with and without gigantoproductines) and the conglomerate. The *Saccaminopsis* packstone, peloidal mudstone, microbialite and microconchid build-ups yield almost no corals. In contrast, the *Gigantoproductus* horizons are quite rich and diverse in rugose corals, which suggests that brachiopods and corals were not in competition and perhaps that corals took advantage of the water flows produced by the filtration systems of the brachiopods the same way that some scleractinian corals and giant clams interact in Recent reefs (Wood, 1999).

(2) Reworking and mixing. As highlighted by Aretz (2001), the conglomerate in parasequence +2 is composed of pebbles showing microfacies known from underlying strata (Fig. 3B), but also microfacies that are not known anywhere in the locality, suggesting of reworking and transportation from outside the outcrop area. Both coral and brachiopod diversity peak within the conglomerate (Table 1), but not only because of obviously reworked specimens. As explained above, many specimens seem to have lived within the pebbles as they do not show any trace of erosion that might be associated to reworking.

(3) Temporal bias. Most of the Royseux taxa were recorded from a single 4<sup>th</sup> order parasequence (100 kyr), and thus, in duration, the diversity is not likely to be related to a long term accumulation, such as those described from the British Isles, Morocco or Spain (see section 5.1.).

(4) Palaeobiogeography. During the Late Viséan, global sea level was high, allowing easy connections and faunal exchange between various palaeogeographic areas, and thus resulting in many widely distributed and even cosmopolitan taxa (Fedorowski, 1981; Sando, 1990). The Namur-Dinant Basin was situated along the southern margin of Laurussia, flooded by the remnants of the Rhenohercynian Ocean and was separated from the Palaeoethys Ocean by Hunic Terranes (Armorica, French Central Massif, Saxo-thuringian and Moldanubian zones, the Turkish Anatolides, etc.; von Raumer et al., 2003). However, exchanges through this 'high' area were possible and marine faunas on both sides are quite similar (European Coral Province of Sando, 1990).

(5) Palaeoclimate. It is generally suggested that high temperatures (either in a greenhouse interval or during interglacials within icehouse intervals) are associated with high diversity (Cecca, 2002) and that high temperature is crucial for the establishment of new species (Berteaux et al., 2010). At global scales, the late Viséan was a time a high marine biodiversity (e.g. Raup & Sepkowski, 1982; Wood, 2001; Kiessling, 2009). This peak is partly explained by tropical conditions prevailing on most of the Palaeoethys Ocean linked to high sea surface temperatures (Kiessling, 2009). The early Carboniferous climate was characterised by progressive cooling and the onset of the Late Palaeozoic Ice Age in the late Viséan (Isbell et al., 2003). However, sedimentary cycles related to glacio-eustatic sea-level changes have been reported from the Belgian platform sections as early as the early Viséan (Mottequin, 2008; Aretz et al., 2011). Similarly, the Middle Devonian and Late Cretaceous are dominated by third-order eustatic sequences that are most probably related to glacio-eustasy (see review by Miller et al., 2005). Both periods recorded warm conditions as proven by the wide carbonate platforms developed at high latitudes. Both periods are also associated with diversity peaks in the marine realm (Kiessling, 2009; Kiessling & Kocsis, 2015).

## 7. Conclusions

Comparisons with other late Viséan fossiliferous sites indicate that the rugose coral fauna of Royseux is highly diverse, whether the entire stratigraphical section or particularly within parasequence +2. However, the diversity of one taxonomic group may not be representative of another group (Price, 2002; Orme et al., 2005), and as such, Royseux is a biodiversity palaeo-hotspot for rugose corals but neither for tabulate corals nor brachiopods or other invertebrates (the latter are still poorly known and further studies could change this view). Outcrop conditions unfortunately preclude correct statistical sampling and in situ population study, such as those of Hubbard (1966) or Aretz (2002).

The origin of the high biodiversity cannot be explained by a single cause. Hence a complex network of global and local causes are necessary, but none of them seems to dominate. However, it is clear that the local influence of tectonics and lithofacies creating numerous micro-environments may explain why the diversity is restricted to a small area and not to the whole Namur-Dinant Basin.

Further comparison with other rich and better known coral sites in the Silurian (e.g. Gotland), Devonian (Ohio) or Cretaceous (Gossau) would possibly provide new insight into the causes of the diversity peak and what controlled the distribution of the other invertebrates.

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