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Famennian and Tournaisian recoveries of shallow water Rugosa following late Frasnian and late Strunian major crises, southern Belgium and surrounding areas, Hunan (South China) and the Omolon region (NE Siberia)

Eddy Poty *

Service de Paléontologie Animale, Université de Liège, Sart Tilman, B18, B-4000 Liège-1, Belgium

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Abstract

The Rugosa remained almost totally absent from the platform environments of southern Belgium and surrounding areas, Hunan and Omolon during the long time interval between the end-Frasnian crisis and the early part of the late Famennian (*marginifera* Zone), probably owing to cool climatic conditions. They first reappear in the Upper *marginifera* Zone, but are uncommon and poorly diversified. Few of them belong to pre-Famennian genera. It is only near the beginning of Strunian time that rugose corals radiated and became common. Their morphological and allometric variabilities were very large, indicating their high potential for adaptation to free niches. This first radiation was abruptly terminated by an extinction event, and a second radiation quickly began, mainly from new taxa and only from a few previously known ones. In western Europe and in Hunan, this second radiation was also stopped abruptly, while species were evolving, by the Hangenberg event at the end of the Strunian. In Omolon, where the position of the Devonian–Carboniferous boundary is doubtfull, the second radiation may have been completed before the end of the Strunian, and probably the corals affected by the end-Famennian event were new ones, resulting from a third radiation. In the three regions and at each recovery, the rugose corals are endemic, indicating that marine connections were poor. After the Hangenberg event, surviving Rugosa reappeared almost immediately (except in South China) and were widespread, indicating good marine connections. However, they remained poorly diversified, sometimes until the late Tournaisian. The two major extinctions (end-Frasnian and end-Famennian) and the Strunian ones were responsible for the major taxonomic differences between pre-Famennian and post-Famennian Rugosa.

Keywords: Rugosa; Late Devonian; extinctions; recoveries; early Tournaisian

1. Introduction

Rugose corals were affected by major extinctions at the end of the Frasnian and at the end of the Famennian (Sorauf and Pedder, 1986; Scrutton, 1988; Sorauf, 1989; Oliver and Pedder, 1994), each followed by recoveries. These events are mainly responsible for the deep differences existing between pre-Famennian and Carboniferous rugose corals; the Famennian ones occupy an intermediate position. Famennian corals include a few previously known taxa and a few which extend into the Carboniferous,

* Fax: 32 43 665338; E mail: e.poty@ulg.ac.be

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but many of the taxa present are restricted to the stage. Some of the latter show a mixture of 'Devonian' and 'Carboniferous' morphological characters — e.g., trabecular septal structure ('Devonian') and the development of an axial structure ('Carboniferous').

The aims of this study are to document the stratigraphic and palaeogeographic distributions of the Famennian and earliest Tournaisian rugose corals from shallow water environments, to emphasize the events affecting these corals, to define their taxonomic relationships and to attempt to specify their evolution. Rugose corals from deep water environments and unrevised reports of shallow water corals are not considered here.

The use of lists of corals to determine the stratigraphy and the palaeogeography of Rugosa is not reliable without revision of their systematics. Indeed, the large specific morphological variabilities of the Rugosa are often so high that they could be assigned to several different species or even genera. Moreover, homeomorphs commonly occur at the species, genus or even family level. These result in an excessive number of described taxa (not only for the Famennian, but for all stratigraphic levels).

Only the study of numerous specimens makes it possible to determine the ranges in variation of species, to precisely define their morphology and to avoid most systematic mistakes. On the other hand, the possibility exists that, after revision, closely related species with overlapping ranges in variations may be assigned to only one species, which could partly explain the low number of taxa recorded here.

2. Setting (Fig. 1)

Areas showing a transition between the Frasnian and the Lower Carboniferous and yielding shallow water rugose coral faunas are not common. The most classic example of such a transition is well exposed on the platform that developed during the Devonian and Carboniferous to the south and east of the Brabant Massif, from northern France, crossing southern Belgium, towards the western part of Germany (called here the Southern Belgium platform) (Fig. 1). The terranes of this region provided the basis for our research on corals and the determination of their history and evolution (Poty, 1984, 1986, and in prep.; Poty and Boland, 1996). The rugose corals of the Devonian–Carboniferous transition were also the subject of systematic and stratigraphic works in Hunan (Poty and Xu, 1996) and in the Omolon region (Poty and Onoprienko, 1984).

Other Famennian, shallow water, rugose corals have been reported and described from Poland (Rozkowska, 1969; Fedorowski, 1991), the former U.S.S.R. (see among others: Gorsky, 1938; Vassiljuk, 1960; Papojan, 1977), Moravia (Galle, 1987) and New Mexico (Sorauf, 1992).

3. Distribution of uppermost Frasnian to lowermost Carboniferous rugose corals

3.1. Southern Belgium and surrounding areas (Fig. 2)

3.1.1. Extinction of upper Frasnian rugose corals

On the Southern Belgium platform, the decline of Frasnian corals begins near the boundary between the *jamieae* and *rhenana* conodont Zones. It is correlated with a rise in sea-level, a cooling of the sea water and the development of argillaceous facies everywhere in the basin. It is first marked by progressive extinction of colonial members of the family Disphyllidae and their replacement with other colonial corals belonging mainly to Phillipsastreidae. This decline ends with the complete disappearance of corals in the *linguiformis* Zone, just below the Frasnian–Famennian boundary and before the Kellwasser event.

3.1.2. Famennian rugose coral recovery

The interval between the base of the *triangularis* Zone (base of the Famennian) and the Upper *marginifera* Zone (lower part of the upper Famennian) seems to be devoid of Rugosa, in shallow water as well as in deeper water facies. Previously, (Poty, 1986) recorded the genus *Neaxon* from the shales of the Famenne Formation (lower Famennian) and *Tabulophyllum*? sp. accompanied by corals resembling *Campophyllum* from the lower part of the upper Famennian. However, a subsequent revision of the specimens and the sections yielding them has not confirmed these records.

The first Famennian shallow water rugose corals

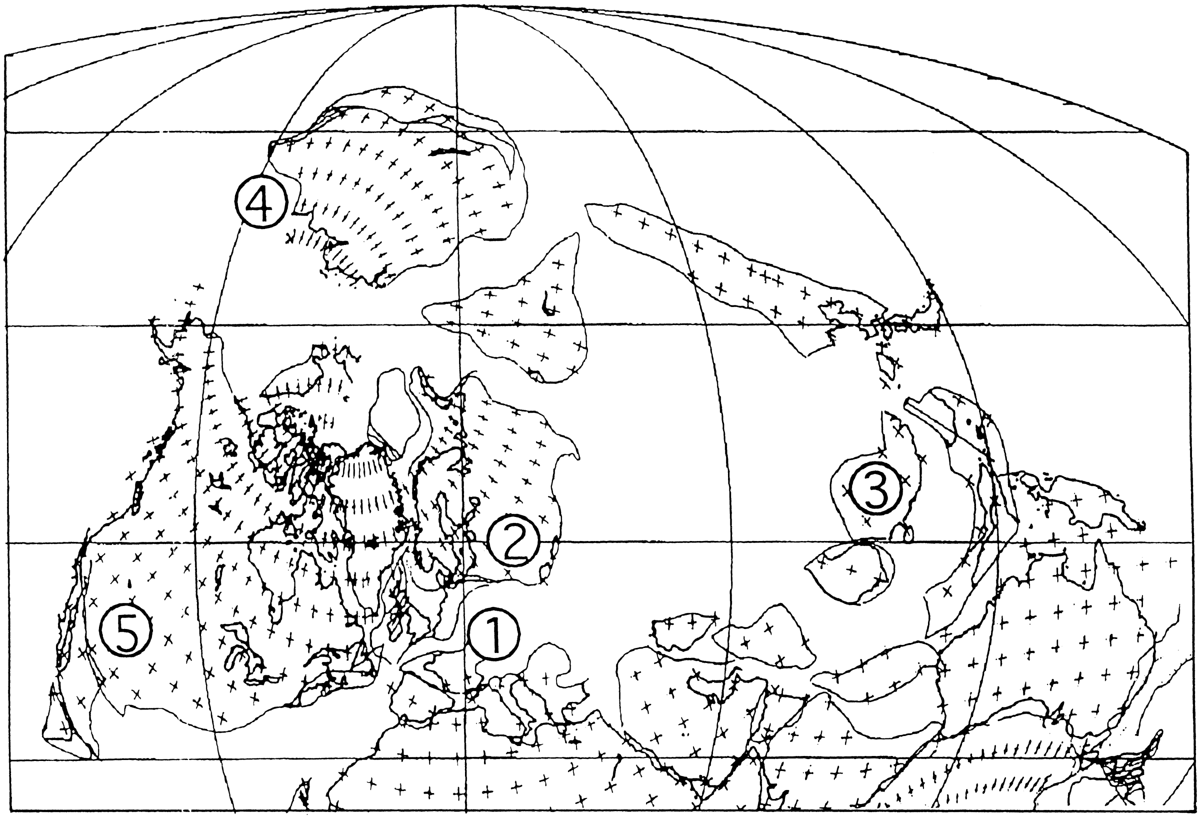

Fig. 1. Distribution of Famennian and lowermost Tournaisian deposits yielding Rugosa and discussed here: *1* = Southern Belgium platform and surrounding areas (Etroeungt area in France, western part of Germany); *2* = Polish Sudetes, Holy Cross Mountains; *3* = Hunan, South China; *4* = Omolon region; *5* = New Mexico. Famennian base map of Scotese and McKerrow (1990).

appear in the Condroz area, in the calcareous siltstones of the Souverain-Pré Formation (Upper and Uppermost *marginifera* Zones), which mark a transition to more open marine environments following the siliciclastic-dominated nearshore environments of the underlying Esneux Formation (*rhomboidea* Zone to Upper *marginifera* Zone) (Fig. 2). These corals are scarce and belong to only two taxa. The first (Chevetogne section, Upper or Uppermost *marginifera* Zone) consists of small, horn-shaped, dissepimented coralla, not yet described. It is a representative (or a homeomorph?) of *Catactotoechus* Hill, which is known from the Famennian of Western Australia (Hill and Jell, 1971). The second (Badon section, Uppermost *marginifera* Zone; Bouckaert and Dreesen, 1976) is a small, undescribed species of *Breviphrentis* Stumm.

Over most of the platform, the Souverain-Pré Formation is overlain by deposits composed mainly of shallow water, subtidal to alluvio-lagoonal sandstones, siltstones and shales, in which no coral has been recorded (Wulff, 1923, figured a cerioid coral showing affinities with *Endophyllum*, that he had found in the Evieux Formation, in the Aachen area in western Germany; the specimen is now missing). However, in the Avesnes area (northern France), the Souverain-Pré Formation is overlain by marine shales of the Sains Formation, which locally contain numerous large, solitary corals belonging to another species of *Breviphrentis*. These corals show a large range of variability in the size and shape of their morphological features, and develop dissepiments associated with periodic constrictions of their calices prior to rejuvenescence (indicating seasonal variations in the environment). Thus, they resemble *Breviphyllum* Stumm, a genus closely related to *Bre-*

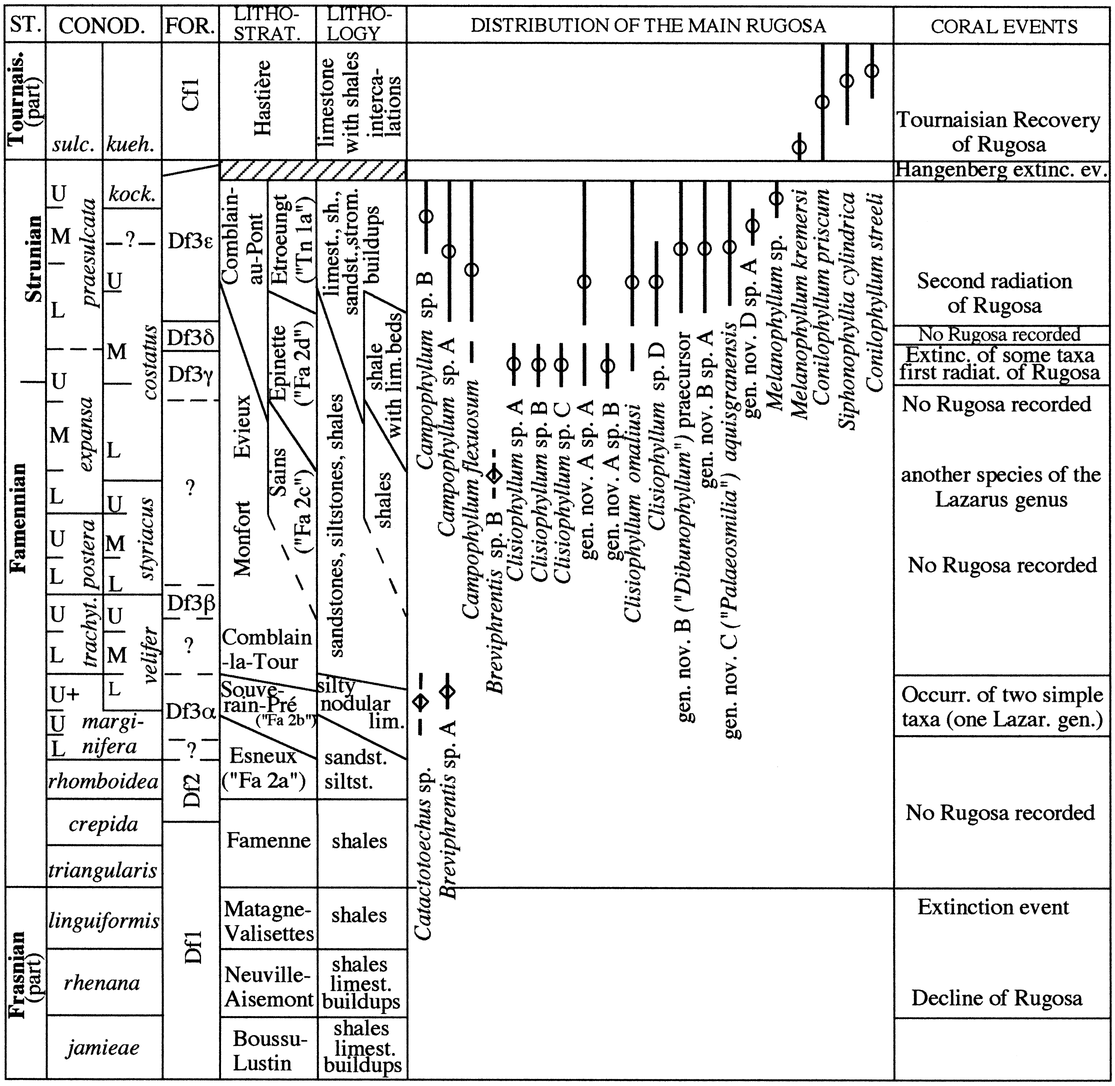

Fig. 2. Stratigraphic distribution of the main Rugosa and events in the Upper Devonian and the lowermost Carboniferous of the Namur–Dinant Basin in northern France, southern Belgium and western Germany. Biostratigraphic data from Conil et al. (1986) and Ziegler and Sandberg (1990). Rhomb: solitary coral with simple morphology. Circle: solitary coral with complex morphology.

viphrentis, but distinguished from the latter by the presence of dissepiments (Hill, 1981; Oliver, 1992). This species could have evolved from the previous species of *Breviphrentis*. It is present in the base of the Avesnelles section, which lies within the lower part of the Lower *costatus* Zone (upper part of Lower *expansa* Zone), but it is not well dated in the other sections from which it is recorded. *Breviphrentis* has never been found either above the Sains Formation, or in the Famennian of any other area.

The genus *Breviphrentis* (and the family Siphonophrentidae Merriam, to which it belongs) was not previously known above the Givetian (Oliver, 1992). Therefore, its reappearance during the Famennian as one of the first corals after the upper Frasnian crisis must be emphasized (note that the closely related *Breviphyllum* is known only from the Lower Devonian).

3.1.3. Strunian radiations

Rugosa become abundant and show a radiation from the lower part of the Epinette Formation, in open marine shales belonging to the upper part of the Df3γ Subzone–lower part of the Middle *costatus* Zone–LV Spore Zone (the base of the latter defining the base of the Strunian Substage; Conil and Lys, 1980; Conil et al., 1986), stromatoporoids also reappear in this interval. This radiation is characterized by the appearance of some corals that developed morphological characters usually typical of Carboniferous taxa. Their phyletic origins are not known. Their very high morphological variability makes them almost impossible to classify. At least seven 'species' belonging to four 'genera' can be defined, with many specimens showing mixed systematic characters (Poty, in prep.). This problem of systematics was also pointed out by Sorauf (1992) in his study of the rugose coral fauna of the Famennian Percha Shale of New Mexico. He recognized the same trends toward the occurrence of Carboniferous types of corals, which led him to assign them provisionally to Carboniferous genera.

Among the trends observed, the development of an axial structure is the most significant. This axial structure varies considerably from a simple columella formed by extension of the counter septum, to complex, spiderweb-like, axial structures comprising an extension of the counter septum, septal lamellae and axial tabellae (clisiophylloid type). In some instances, within one specimen, the axial structure may be discontinuous and may develop several stages of complexity. The axial structure originated in a species probably belonging to the caninoid *Campophyllum* Milne-Edwards et Haime, a genus which is typical of the Strunian on the Southern Belgium platform, and may possibly have developed in other taxa as well. This trend, among others, gave rise to species similar to those of the genus *Neoclisiophyllum* Wu (in Yü et al.), known from the Viséan and Namurian of Eurasia, and to two other species, one of which shows affinities with *Clisiophyllum omaliusi* Haime, and the other with '*Dibunophyllum*' *praecursor* Frech.

Most of these Rugosa disappear in the lower part of the Df3δ Subzone, along with an increase in the calcareous content of the deposits. Some, however, gave rise to those reappearing in a second radiation, from the uppermost Df3δ to the lower part of the Df3ϵ Subzone (uppermost part of Epinette Formation). This occurred after an interval devoid of corals.

Some of the most common corals of the second radiation were formerly described as *Campophyllum flexuosum* (Goldfuss), *Clisiophyllum omaliusi* Haime, '*Dibunophyllum*' *praecursor* Frech, and '*Palaeosmilia*' *aquisgranensis* (Frech), but numerous other taxa, undescribed or mistaken for those listed, are also present. Among them are *Melanophyllum* sp. and a genus (gen. nov. D sp. A) closely related to *Tabulophyllum*, but having an axial structure. All of these corals show variabilities as high as those of the previous ones.

The main radiation affected *Campophyllum* and originated from *C. flexuosum*, or from forms closely related to it. *C. flexuosum* is a common species from the top of the Df3γ Subzone to the top of the Df3ϵ Subzone. It is dominant in the coral assemblages of the eastern part of the platform (Vesdre–Aachen area) and has an intraspecific variability as great as the variability usually observed at the interspecific level (see Poty, 1984, pl. 2, figs. 1–3). This variability affects not only the size and the morphology of the mature stages, but also the ontogeny.

An increase in the diameter and in the number of septa is one of the trends commonly observed; it corresponds here to a hypermorphosis (McNamara, 1986; Poty, 1993). This process gave rise very rapidly, as early as the beginning of the radiation, to a large species, *C.* sp. A (= *Campophyllum* sp. Poty, 1984, pl. 2, fig. 4), with a diameter reaching approximately three times the diameter of the ancestor. This trend continues to occur in *C. flexuosum*, at different stratigraphic levels and in different localities. *C.* sp. A also shows very large variability, for instance in the length and thickness of major septa, and in the shape of tabulae, which may be split. In the lower part of the Df3ϵ Subzone, this species or perhaps another large form of *C. flexuosum* probably gave rise, to '*Palaeosmilia*' *aquisgranensis*, a homeomorph of the Viséan–Namurian genus *Palaeosmilia*. The morphological characters of the Strunian '*Palaeosmilia*' are very close and sometimes identical to those of the Viséan *P. murchisoni* Milne-Edwards et Haime, but the microstructure of the skeleton is different, resembling that in *Campophyllum*. It is noteworthy that '*P.*' *aquisgranensis* usually developed in very shallow water environments, as did *P. murchisoni*.

Another trend in the variability of *C. flexuosum* is characterized by the development of angular, then of lateral dissepiments, giving rise to a more complex dissepimentarium. This trend, together with an increase in size, also gave rise to a new taxon, *C.* sp. B (= gen. and sp. nov. A of Poty, 1984, pl. 2, fig. 5), which is common at the top of the Strunian.

Thus, *C. flexuosum* rapidly gave rise to other, very different, species. This high variability and rapid evolution illustrate the radiation of a colonizing species having a large potential for adaptation, in many new, free niches.

3.1.4. Devonian–Carboniferous boundary event and the early Tournaisian recovery

The Hangenberg event, at the Devonian–Carboniferous boundary, corresponds to a sea-level fall which is usually marked by a gap in the stratigraphic series on the platform. It caused the extinction of almost all western European upper Strunian coral taxa and numerous other groups, such as phacopid trilobites and stromatoporoids. The recovery of the latter was at its height and they had begun to construct biostromes in the Vesdre area. Among the Rugosa, the only survivors were *Melanophyllum*, which reappeared immediately after the crisis, and *Clisiophyllum* which reappeared later, in the early Viséan. Indeed, some specimens of *Clisiophyllum omaliusi* (also highly variable) are very similar to some lower Viséan representatives of *Clisiophyllum*, even in their microstructure. However, because no species of *Clisiophyllum* is known in the Tournaisian, the possibility must be considered that the Viséan *Clisiophyllum* could be homeomorphs of the Strunian ones. However, note that some members of the same Carboniferous family are recorded at least from the middle Tournaisian (such as *Eostrotion* Vaughan; see for example in Poty and Xu, 1996).

The chronology and modalities of the recovery of rugose corals after the Hangenberg event are very different from those following the end-Frasnian crisis. On the Southern Belgian platform (and worldwide), Tournaisian rocks are mainly composed of limestones, in contrast with the Famennian sedimentary pattern, where siliciclastics were dominant. That difference corresponds to a global change which followed the Hangenberg event.

Two species of corals reappeared at the beginning of the Tournaisian, just after the crisis: *Conilophyllum priscum* (Münster) and *Melanophyllum kremersi* (Poty). The first is recorded as low as the top of the *praesulcata* Zone (therefore below the Devonian–Carboniferous boundary) in the deep water facies of Germany (Weyer, 1994). It is present in the Strunian of the Omolon region (see the discussion below of the position of the Devonian–Carboniferous boundary in that region). *C. priscum* is an opportunistic species, showing a very high rate of morphological variability, which colonized deep water as well as shallow water environments. It is known from as far away as the Western Interior Province of North America (Sando and Bamber, 1985). *Melanophyllum kremersi* belongs to a genus (closely related to, and possibly synonymous with *Kizilia* Degtyarev) which is widespread in Eurasia, from the Tournaisian to the Namurian, but is usually uncommon on the inner platforms. *Melanophyllum* is known from the uppermost Strunian (Poty, 1984, pl. 2, fig. 6). Closely related colonial forms (*Melanophyllidium*) are also known in Omolon, from levels of the same age as those of *Conilophyllum priscum* (Poty and Onoprienko, in Shilo et al., 1984). *Melanophyllum kremersi* has a very short stratigraphic range on the Southern Belgium platform, being limited to a few beds overlying the event unconformity.

Not long after these occurrences, *Siphonophyllia cylindrica hasteriensis* (Salée) developed. *Siphonophyllia* is a common genus up to the lower part of the upper Tournaisian (Yvoir Formation, Cf2 Zone, *communis carina* Zone). It is known in the Upper Famennian (Df3γ Subzone) of the Omolon region (Poty and Onoprienko, in Shilo et al., 1984).

A little later, *C. priscum* gave rise, through a hypermorphosis process (Poty and Boland, 1996), to *C. streeli* Poty et Boland. This species is a homeomorph of the genus *Siphonophyllia* and was previously mistaken for it (Poty, 1984).

The two species of *Conilophyllum* disappeared at the top of the Hastière Formation (Cf1α, α' Subzones, correlated with the *duplicata* and *cooperi* Zones), following the development of argillaceous deposits (Pont d'Arcole Formation, lower part of the Cf1$''$ Subzone, lower part of the *obsoleta* Zone, RC1γ Coral Zone). Meanwhile, *Uralinia lobata* Poty et Boland appeared, along with two small non-dissepimented corals of deep water origin: *Cyathaxo*-

nia cornu Michelin and *Saleelasma delepini* Weyer, marking the base of the RC1γ Coral Subzone. *Uralinia* appeared at the same time in South China and probably evolved from *Siphonophyllia* (Poty and Xu, 1996). *C. cornu* is known in the Famennian deep water facies of Poland (Rozkowska, 1969) and Germany (Weyer, 1984). It is a long-ranging species, which extends at least up to the Namurian. Thus, the Rugosa remained poorly diversified until the early part of the late Tournaisian when a more diversified fauna developed.

Therefore, corals belonging to previously known genera reappeared immediately or shortly after the Hangenberg event and some gave rise to new species. However, in western Europe, they did not show such high radiation as during the late Famennian (Strunian) recovery, possibly because environments on the carbonated platform were not favourable for the development of benthic faunas, as suggested by the systematic poverty of other groups such as foraminifers and brachiopods.

3.2. Hunan, South China (Fig. 3)

The Famennian and lower Tournaisian rugose corals of Hunan have been the subject of works mainly by Yü (1931,Yü, 1934), Fan (1963), Wu et al. (1981), Yan (1982) and Tan et al. (1987). The systematics and stratigraphic distribution of most of them were recently revised by Poty and Xu (1996). The fauna which developed during the Upper Famennian is totally different from that which occurred at the same time in western Europe and in Omolon. Correlations with these regions are mainly based on foraminifers, conodonts and sequence stratigraphy (Hance et al., 1994) (Fig. 3).

Many of the Rugosa extended higher in the Frasnian in South China than in western Europe, and the last Frasnian taxa, including *Disphyllum* and *Hexagonaria*, disappeared with the end-Frasnian event (Hou et al., 1996; Muchez et al., 1996a). Above that level, rugose corals are almost absent from the lower and middle parts of the Famennian, from which only a few solitary corals have been recorded (Hou et al., 1996). They need to be revised to clarify their systematic and stratigraphic positions.

Corals are definitely present in the Shaodong Formation (Middle *expansa* Zone, Df3β Subzone; Tan et al., 1996; Hance, 1996), usually in argillaceous limestones intercalated in the sandstones, siltstones and shales which compose most of the formation. They are solitary corals belonging to possibly no more than four species assigned to four genera: *Ceriphyllum elegantum* Wu et Zhao, cf. *Circellia* sp., *Complanophyllum compressum* Wu et Zhao and *Eocaninophyllum shaodongense* (Wu et Zhao) (Wu et al., 1981; Poty and Xu, 1996).

The Shadong Formation represents a transitional phase from siliciclastic-dominated nearshore towards more open marine environments. The overlying Menggongao Formation (Df3γ–Df3ϵ Subzones) is mainly composed of limestones and shales representing fully open marine conditions (Muchez et al., 1996b; Hou et al., 1996). It could correspond more or less to the Strunian Substage.

In the lower part of the Menggongao Formation, corals became common and more diversified. They include some of the previous species (*Complanophyllum compressum* and *Eocaninophyllum shaodongense*) and also new ones: *Eocaninophyllum yizhangense* (Zuo), which is the type species for the *E. yizhangense* Zone (= *Caninia dorlodoti* Zone of Wu et al., 1981), *E. stereoseptatum* (Wu et Zhao), *E.* sp., *Smithiphyllum antiquatum* (Wu et Zhao), *Dematophyllum minor* (Wu et Jiang) and *D. hunanense* (Wu et Jiang). *Eocaninophyllum* is the most common taxon and its species are affected by very great morphological variability which is an expression of their radiation (but makes their systematics difficult).

The genera in the lower part of the Menggongao Formation have a very short stratigraphic range and they disappeared before the occurrence of *Cystophrentis*, the type genus of the *Cystophrentis* Zone of Yü (1931). *E. yizhangense*, which extended a short distance into this zone, is the exception. No major sedimentological change was recognized during this coral event. The first *Cystophrentis* appear in the middle part of the Menggongao Formation, at levels situated within the Df3δ or the lower part of the Df3ϵ Subzone (Hance, 1996). They belong to two closely related species (*C. kolaohoensis* Yü and *C. xinhuaensis* Jiang), which are the probable ancestors of the younger species of *Cystophrentis*. The latter are the only other corals actually recorded from the zone (Poty and Xu, 1996). In the studied sections, *Cystophrentis* disappears near the top of the Menggongao

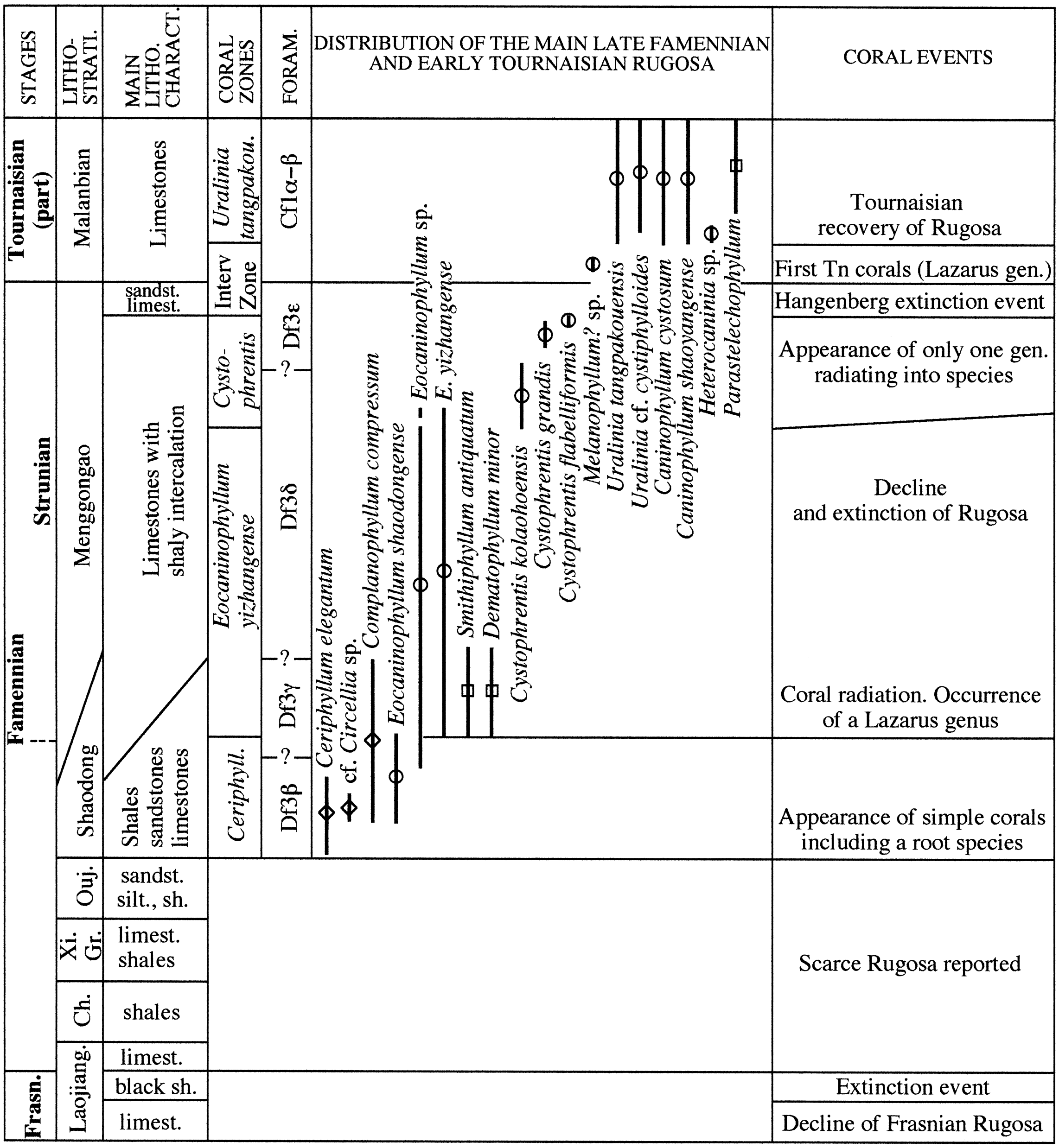

Fig. 3. Stratigraphic distribution of the main Rugosa and events in the Upper Devonian and the lowermost Carboniferous in Hunan (South China), from Poty and Xu (1996). Biostratigraphic data from Hance et al. (1994) and lithostratigraphy from Tan et al. (1996). *Laojiang.* = Laojiangchong; *Ch.* = Changlongjie; *Xi. Gr.* = Xikuangshan Group; *Ouj.* = Oujiachong. Rhomb: solitary coral with simple morphology. Circle: solitary coral with complex morphology. Square: colonial coral.

Formation, just below siliciclastic beds (in nearshore areas) or fenestral limestones (in the vicinity of the platform) which cap the formation. These levels were deposited in response to an important drop in sea-level (Hance et al., 1994) and can be correlated with the Hangenberg Shale of the German sections.

The coral genera of the Shaodong and Menggongao formations are restricted to the Famennian and their origins are unknown, except for *Smithiphyllum*, which is known before the end-Frasnian crisis in the Frasnian of North America, China, Timan and Armenia (McLean and Pedder, 1987). None of these corals were recorded from the Famennian outside China and Southeast Asia; the report of *Cystophrentis* from Armenia (Papojan, 1974) cannot be regarded as a certainty and should be verified.

After the Hangenberg event, the lowest part of the Malanbian Formation, partly included in the Cf1α Subzone, is almost devoid of rugose corals and only a few specimens, assigned with some doubt to *Melanophyllum*, have been found. Rugose corals became common approximately at the boundary between the Cf1α and the Cf1β Subzones. They include *Uralinia tangpakouensis* (Yü), the type species for the *U. tangpakouensis* Zone, the base of which can be correlated with the base of the RC1γ Coral Subzone of western Europe (Poty and Xu, 1996). The species recorded in this zone belong to genera that are known outside China (*Uralinia*, *Caninophyllum* and ?*Eostrotion*), are closely related to a widespread genus (*Parastelechophyllum* Poty et Xu, a probable geographical variant of *Stelechophyllum* Tolmachev), or are endemic (*Heterocaninia*). They mark the first coral radiation after the Hangenberg event.

3.3. Omolon (Fig. 4)

3.3.1. The Famennian coral recovery

The oldest Famennian rugose corals appear in the Perevalny and Andylivan suites, in the Df3β Subzone, *obliquicostatus* Zone of Gagiev (1979; see also in Shilo et al., 1984), a local conodont zone partly equivalent, according to the author, to the *styriacus* Zone (and therefore to the *postera* Zone). They consist of at least two species which were assigned to *Tabulophyllum* (*Tabulophyllum simakovi* Poty et Onoprienko) and, with some doubt, to *Nalivkinella*. The first genus was common during the Frasnian. They do not extend into higher levels in Omolon (Fig. 4).

From the lower part of the Gytgynpylgin Suite (lowermost Df3γ Subzone, lower *delicatus* Zone of Gagiev), the corals listed above are succeeded by *Siphonophyllia latetabulata* Onoprienko (the oldest representative of the genus). Then, from the boundary between the *delicatus* and *inornatus inornatus* Zones, there appear other solitary corals doubtfully assigned to *Gorizdronia* and *Campophyllum*, and an undetermined caninoid species. These Rugosa are common and truly mark the first Famennian coral recovery in the region. They became extinct at the boundary between the *inornatus inornatus* and *parapetus* Zones, in the lower Df3ϵ Subzone. They were replaced by new coral taxa, as common as the preceding ones, including mainly *Molophyllum magnum* Onoprienko, *M. adapertum* Onoprienko, two undetermined species developing an axial structure, and another undetermined caninoid species.

This second fauna became extinct at the boundary between the *inornatus rostratus* and *lenticularis* Zones, and was also replaced immediately by a new one. The latter includes mainly *Parasiphonophyllia smirnovi* Onoprienko, *Conilophyllum* cf. *priscum* (Münster), and two colonial species belonging to *Melanophyllidium*. Except for *Parasiphonophyllia*, these genera are known, or are closely related to corals known, in the Famennian or Carboniferous outside Omolon.

The third coral fauna became extinct, together with stromatoporoids, *Quasiendothyra* and *Icriodus*, at the top of the Elergetkhyn Suite. A poorly diversified fauna, including common *Siphonophyllia* aff. *cylindrica* and rare caninoids and cf. *Amplexus*, occurs in the overlying levels.

All the corals that are common in the strata listed above show great morphological variability, leading to difficulty in systematics and comparisons with foreign taxa.

3.3.2. Stratigraphy of the Famennian and lowermost Carboniferous deposits of Omolon

Some confusion exists concerning the stratigraphy and dating of the Famennian and Lower Carboniferous of the Omolon region. Indeed, they are based mainly on a local conodont zonation established by Gagiev (1979, see also in Simakov et al., 1983), and tentatively correlated with the conodont zonation of Sandberg (1979). In particular, the doubtful assignment of a poorly preserved conodont fragment to *Siphonodella sulcata* (Hance, 1996), led to the conclusion that the D/C boundary must be situated below bed II-21 of the Ustyevoy section II (in the *lobatus* local Zone, within the Elergetkhyn Suite). Consequently, 'Devonian taxa', including

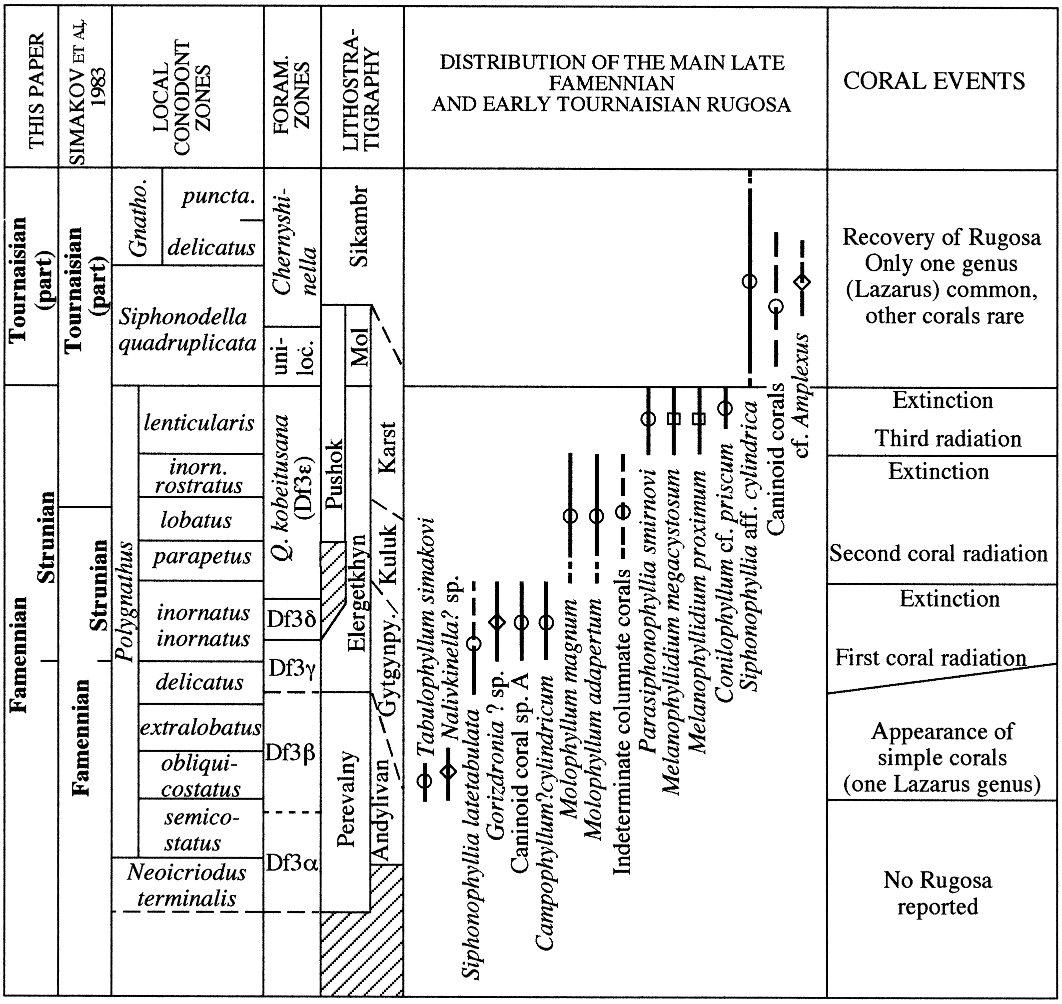

Fig. 4. Stratigraphic distribution of the main Rugosa and events in the Famennian and the lowermost Carboniferous of Omolon. Lithostratigraphy and biostratigraphy from Simakov et al. (1983). Rhomb: solitary coral with simple morphology. Circle: solitary coral with complex morphology. Square: colonial coral.

stromatoporoids, the foraminiferan genus *Quasiendothyra* and the conodont genus *Icriodus*, which became extinct world-wide at the end of the Devonian, crossed Gagiev's D/C boundary and were considered to be local survivors (Simakov et al., 1983; Shilo et al., 1984). However, neither a sedimentological nor a biological event that could correspond to the Hangenberg event, as observed elsewhere, has been reported immediately below Gagiev's boundary. Therefore, there is no reliable argument to support this position for the Devonian–Carboniferous boundary. Concerning the Rugosa, extinction events are reported either lower, at the boundary between the *inornatus inornatus* and *parapetus* local conodont Zones (extinction of the *Siphonophyllia latetabulata* assemblage), or higher, between the *inornatus rostratus* and *lenticularis* Zones (extinction of the *Molophyllum* assemblage) and between the *lenticularis* and *quadruplicata* Zones (extinction of the *Parasiphonophyllia* assemblage).

It is more likely that the extinction of the *Parasiphonophyllia* coral assemblage, which matches the extinction of stromatoporoids, quasiendothyrids and *Icriodus*, could correspond to the Hangenberg event.

Therefore, the Devonian–Carboniferous boundary should be situated much higher than previously placed, at the boundary between the Elergetkhyn Suite and the Mol Suite (between the *lenticularis* and *quadruplicata* Zones). This interpretation agrees with the fossils reported from the overlying levels: (1) foraminifera are poor and belong to the 'unilocular assemblage' which is characteristic of the lowermost Tournaisian Cf1α Subzone in western Europe (Conil et al., 1991) and in South China (Hance et al., 1994; Hance, 1996); (2) the only common Rugosa recorded is close to *Siphonophyllia cylindrica*, a coral appearing in the lower Tournaisian of Belgium (Poty and Boland, 1996); (3) typical Tournaisian conodonts (except the doubtful *Siphonodella sulcata*) only begin to appear (see in Shilo et al., 1984).

This implies that the corals (*Conilophyllum*, *Melanophyllidium*) of the *Parasiphonophyllia* assemblage, which were reported outside Omolon from the Carboniferous only, are older here.

4. Other shallow water Famennian rugose coral faunas

4.1. Poland

A Famennian coral fauna was described by Rozkowska (1969) from the *marginifera* to *costatus* Zones of the Holy Cross Mountains. It includes mainly deep water, small, solitary corals without dissepiments, but also contains dissepimented solitary and colonial forms. Some of these corals could have been reworked from older, pre-Famennian, deposits, and others have been misidentified (Poty, 1986). Therefore, this fauna is not considered here.

Two compound corals were described by Fedorowski (1991) from the *Quasiendothyra kobeitusana* Subzone (Cf3ϵ) of the Sudetes. The affinities of the first, *Sudetiphyllia* Fedorowski, are not known. It is considered by Fedorowski to be one of the oldest members of the family Stylostrotionidae Fedorowski (= Heterostrotioninae Poty and Xu, 1996, excluding *Stylostrotion* Chi, which is a member of the Lithostrotioninae). Its coralla are thamnasterioid to aphroid, suggesting that it is a relatively advanced genus, because such patterns usually develop from cerioid ancestors. The second coral described by Fedorowski was assigned to *Stylotrotion* Chi, but was reassigned to *Heterostrotion* by Poty and Xu (1996). It is the oldest representative of this genus, which developed mainly during the late Tournaisian and the early and middle Viséan of South China. As for *Sudetiphyllia*, its origin is unknown. These two genera have not been recorded in the Famennian outside Poland. 'Strunian' shallow water solitary dissepimented Rugosa showing affinities with western European corals have also been found in Poland. They are presently being studied by Berkowski (in prep.).

4.2. New Mexico

An abundant rugose coral fauna, described by Sorauf (1992), occurs in the Box Member of the Percha Shale of southwestern New Mexico. It is composed of dissepimented solitary forms and a non-dissepimented, very simple species (only one specimen recorded), assigned to *Gorizdronia* Rozkowska. Some of the dissepimented corals resemble Strunian species of the Southern Belgium platform, but the Percha Shale fauna belongs to the Lower *expansa* Zone and therefore is older. This suggests that some of the Strunian western European corals could have originated from North America, or from the same unknown ancestral stock of species. The species of the Percha Shale show a very high range of variability, making their systematics difficult. None of the taxa is formally known outside New Mexico, or in levels below or above the Percha Shale, except *Gorizdronia*, which is a genus reported from the Famennian of Poland, the Urals and Omolon. However, because of the extreme simplicity of its morphological characters, the coral assigned to *Gorizdronia* could be a homeomorph.

5. Interpretation

5.1. Rugose coral extinctions and recoveries from the end-Frasnian to the early Tournaisian

5.1.1. First Famennian rugose coral recovery

As illustrated in the regions studied and by published data, after the Late Frasnian coral extinction, there was a very long interval during which rugose corals were almost totally missing from the shallow marine platforms. This interval ranges from the base of the Famennian to at least the *marginifera* Zone and, from estimates based on conodonts by Ziegler and Sandberg (1990), could have had a duration of approximately 4 to 5 million years. Thus, the Rugosa (and Tabulata?) reappeared long after most other groups, whereas stromatoporoids recovered usually still later. Note that after the Frasnian crisis, tabulate corals never recovered their position: they were not common during the Famennian and remained relatively poorly diversified until their final extinction during the Permian. The lack of corals during the Early Famennian was probably caused mainly by cool climatic conditions and associated argillaceous-dominated environments and in addition, by the development of restricted marine environments.

In the three regions investigated, the Rugosa reappeared first on the Southern Belgium platform (Upper and/or Uppermost *marginifera* Zones, Df3α Subzone), then in the Omolon region (Df3β Subzone, possibly equivalent to the *postera* Zone), and still later in Hunan (as late as the Df3β Subzone, Middle *expansa* Zone).

The re-establishment of corals can be correlated everywhere with the development, after siliciclastic-dominated nearshore conditions, of more open marine environments (still mainly siliciclastic, but including limestones). The Rugosa reported are exclusively small, simple, solitary species, with or without dissepiments. As suggested by their simple morphology (Hill, 1981), they may have migrated from deeper water and were probably the only Rugosa which were able to adapt to the new environments. Most of them are endemic, except for *Catactotoechus*, which is almost certainly present simultaneously in the Famennian of Belgium and Australia, and for *Nalivkinella* (with some doubt concerning the assignation of Omolon specimens), which is also known in the Famennian of Poland and the Urals (Rozkowska, 1969). Two species belonging to two genera (*Tabulophyllum* and *Breviphrentis*) are reported in pre-Famennian deposits, whereas the origin of the others is not known.

The stratigraphic ranges of these newly re-established corals are relatively short. They disappeared:

(1) on the Southern Belgium platform, as early as the Early *trachytera* Zone, with the incoming of siliciclastic nearshore to lagoonal environments (Condroz facies); Rugosa remained absent to the top of the Lower *costatus* Zone (Upper *expansa*, lower part of Df3γ Subzone), except for a brief occurrence, in the lower part of the Lower *costatus* Zone (Lower *expansa*), of another species of *Breviphrentis*, possibly arising from the former;

(2) in Omolon, in levels correlated by Gagiev (in Shilo et al., 1984) with the upper part of the *styriacus* Zone (*postera*);

(3) in Hunan, gradually from the upper part of the Df3β to the top of the Df3γ Subzones (by correlation, from the Middle to the Upper *expansa* Zones), with the development of more calcareous marine environments, and are succeeded continuously by other Rugosa.

5.1.2. Early Strunian coral radiation

In conjunction with a rise in sea-level and probable climatic warming, new rugose coral faunas developed, beginning approximately at the base of the Strunian Substage, on the Southern Belgium platform, in Hunan and Omolon (the rugose coral fauna of the Percha Shale of New Mexico developed earlier, in the Lower *expansa* Zone). On the Southern Belgium platform and in Omolon (and New Mexico), rugose coral faunas include mainly dissepimented, solitary corals (only a few specimens of non-dissepimented corals have been recorded); in Hunan, both solitary and colonial forms developed. Their morphologies are more complex than those of the previous faunas. They have no relationship to these, except in Hunan, where there is continuity with the previous fauna, and species of *Eocaninophyllum* arise from an older species of the genus. They correspond to morphotypes of environments that are shallower than those of the previous ones, which suggests that they probably migrated from this type of environment and not from deeper habitats.

Their Frasnian ancestors or related taxa are not known (except for the Hunan species of *Smithiphyllum*, a genus widespread during the Frasnian), probably because their characters have been so greatly changed by evolution that reliable comparisons cannot be made. Most of these corals have a large range of variation and some of them radiated into several species. They suffered an extinction near the Df3δ–Df3ε boundary and were succeeded by a new coral recovery. This extinction, relatively major for Rugosa, indicates that Strunian environments were unstable and were subjected to large, probably climatic, changes.

5.1.3. Second Strunian rugose coral radiation

On the Southern Belgium platform, the recovering faunas include species previously present in the early part of the Strunian, which rapidly gave rise to new taxa, and others without apparent relationship to previous ones. In Omolon and Hunan, they are composed only of corals of this last type. All are dissepimented, solitary corals, but in Poland, colonial corals are reported from the Df3ϵ Subzone (Fedorowski, 1991). All these faunas were also endemic.

In southern Belgium and in Hunan, the radiation of these late Strunian rugose coral faunas was stopped by the Hangenberg event, and only two genera survived it (*Clisiophyllum* and *Melanophyllum*).

5.1.4. Third Strunian rugose coral radiation

In Omolon, if the position of the Devonian–Carboniferous boundary is situated higher than previously stated (Simakov et al., 1983), as suggested above, a third extinction affected the whole of the rugose coral fauna in the upper part of the Df3ϵ Subzone. Immediately after it, a new fauna developed, which also seems to have no relationship to the previous fauna. It is composed of shallow water, solitary and colonial species. The latter belong to *Melanophyllidium*, a genus closely related to the solitary genus *Melanophyllum*, which occurred at the same time in southern Belgium. This coral fauna became extinct locally, together with stromatoporoids, *Quasiendothyra* and *Icriodus*, probably owing to the Hangenberg event. Elsewhere, however, some elements of the fauna survived the event and are reported from the Lower Carboniferous.

5.1.5. The Lower Carboniferous rugose coral recovery after the Devonian–Carboniferous boundary event

As outlined above, several recoveries and extinctions affected Rugosa during the time interval of probably less than 2 millions years that spans the Strunian. Most of the last Strunian rugose corals disappeared everywhere at the Hangenberg event, situated just below the Devonian–Carboniferous boundary. The recovery began immediately after the event in the shallow environments of the three studied regions, as it did in the deep environments of Germany (Weyer, 1994). The recovering coral faunas were poorly diversified, but relatively widespread. They included genera or even species which were previously known in southern Belgium and surrounding areas (*Melanophyllum*), or in Omolon (*Conilophyllum priscum*, *Siphonophyllia*). It is about from the *crenulata* Zone that the rugose coral faunas became more diversified (Poty and Boland, 1996; Poty and Xu, 1996).

5.2. Nature of the recovering rugose coral faunas

Two main categories of Rugosa can be recognized in the recovering assemblages of the platform environments of southern Belgium and surrounding areas, Hunan and Omolon: species belonging to Lazarus genera and new taxa of unknown origin.

The Lazarus taxa are few. They include simple, solitary corals (*Breviphrentis*, *Tabulophyllum*), which possibly survived the extinction in relatively deep water environments, and a colonial coral (*Smithiphyllum*), which possibly survived in shallower environments. They reappeared in different areas, at times when environments became propitious for them (but not necessarily for other taxa). The persistence of their morphological characters, with only minor changes, through a long time period (since Givetian for *Breviphrentis* and at least since the end-Frasnian event for the two others), indicates that their characters evolved only a little (at a specific level), suggesting both that they took refuge in relatively stable areas and that they were relatively stable taxa. Their short stratigraphic ranges after their reappearance in the Famennian and their final extinction suggest that they were not able to adapt rapidly to environmental changes.

On the other hand, most of the other taxa are very different from the pre-Famennian ones and their origins are not known. They show a large range of allometric and morphological variations, at the individual, population and specific levels. These variations, which affected among other features the number of septa, the corallite size, and the complexity of the axial structure, dissepiments and tabulae, are mainly of the heterochronic type. But others, affecting the thickness of the skeleton, the length of septa or the vertical shape of the axial structure, and occurring during the ontogeny as well as in the mature stage, could be more directly related to ecological variations. These suggest that their ancestors, after having survived the extinction event in geographic refugia, continued to evolve and changed enough to lose their ancestral characters (up to the family level). It is these taxa which radiated during the Famennian, sometimes giving rise, very quickly, to new genera — e.g., the evolution of gen. nov. C (‘*Palaeosmilia*’) *aquisgranensis* from a species of *Campophyllum*. Extinctions affected most of them during active evolution, before their morphologies were stabilized.

During the Famennian, almost all of the species which developed in each recovery are different from one area to another. This endemism of the Rugosa suggests poor marine connections, probably caused by low sea level. In contrast, the recovering Tournaisian rugose corals, after the Hangenberg event, are widespread, indicating good marine connections and a rise in sea level. Ancestors of the early Tournaisian corals are present in the Strunian of the Omolon region (*Siphonophyllia* and probably *Conilophyllum*) and in the uppermost part of the Strunian of southern Belgium and surrounding areas (*Melanophyllum*).

6. Conclusion

In the investigated regions, Rugosa reappeared briefly in the *marginifera* Zone, long after the end-Frasnian extinction. This was probably the result of relatively cool conditions on the platforms. They are rare, simple, solitary species of a deep water type, only two of which belong to previously known genera (Lazarus taxa). The recovery actually started, on the shallow water platforms, near the base of the Strunian Substage. The recovering Rugosa include mainly complex solitary and a few colonial species. Most of them are new and only one belong to pre-Famennian, Lazarus taxa. They show a large range of variation and evolve rapidly. An extinction event abruptly ended this radiation and was followed by a new coral recovery. This includes some previous taxa (but not the pre-Famennian, Lazarus types) and many new ones, with both groups again showing a large range of variation and a high potential for speciation. A second extinction event followed by a new recovery occurred in the Omolon region in the late Strunian. The Hangenberg event killed most of the Strunian coral faunas. Unlike the Famennian recovery, there was an immediate reappearance of Rugosa after the event and many of them can be related to Lazarus taxa. However, they did not diversify as widely and rapidly as during the Strunian.

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