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The History of Devonian-Carboniferous Reef Communities: Extinctions, Effects, Recovery

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KEYWORDS: PALEONTOLOGY – PALEOECOLOGY – EXTINCTION – REEF-GUILDS – STRUCTURE – DEVONIAN-EARLY CARBONIFEROUS

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SUMMARY

Analysis of the taxonomic composition, diversity and guild structure of five "typical" reef and mud mound communities ranging in age from Late Devonian-Early Carboniferous indicates that each of these aspects of community organization changed dramatically in relation to three extinction events. These events include a major or mass extinction at the end of the Frasnian; reef communities were also effected by less drastic end-Givetian and mid-late Famennian extinctions of reef-building higher taxa.

Peak Paleozoic generic diversities for reef-building stromatoporoids and rugose corals occurred in the Eifelian-Givetian; reef-building calcareous algal taxa were long-ranging with peak diversity in the Devonian. These three higher taxa dominated all reef-building guilds (Constructor, Binder, Baffler) in the Frasnian and formed fossil reef

communities with balanced guild structures. The extinction of nearly all reef-building stromatoporoids and rugose corals at the end of the Frasnian and the survival of nearly all calcareous algae produced mid-late Famennian reef communities dominated by the Binder Guild. Despite the survival of most calcareous algae and tabulate corals, the mid-late Famennian extinction of all remaining Paleozoic stromatoporoids and nearly all shelf-dwelling Rugosa brought the already diminished Devonian reef-building to a halt. These Devonian extinctions differ from mass extinctions by the absence of a statistically significant drop in taxonomic diversity and by their successional and cumulative effects on reef communities.

Tournaisian mud mounds contain communities markedly different from the frame-building communities in Late Devonian and Visean reefs. Mound-building biotas consist of an unusual association dominated by erect, weakly skeletonized members of the Baffler Guild (chiefly fenestrate Bryozoa; Pelmatozoa) and laterally expanded, mud-binding algae/stromatolites and reptant Bryozoa. The initial recovery to reefs with skeletal frameworks in the Visean was largely due to the re-appearance of new species of abundant colonial rugose corals (Constructor Guild) and fenestrate Bryozoa.

This Frasnian-Visean evolution in the taxonomic composition and structure of the reef-building guilds is also expressed by abrupt changes in biofacies and petrology of the reef limestones they produced. Thus, "typical" Frasnian reef limestones with balanced guild structures are framestones-boundstones-bafflestones, Famennian reefs are predominantly boundstones, Tournaisian mud mounds are bafflestones and Visean reefs are bafflestones-framestones.

1 INTRODUCTION

1.1 Extinction events

The tremendous influence of mass extinction events and intervals on the Phanerozoic history of the Earth's biota has been documented in countless paleontologic studies during the last 150 years. However, interest in these events escalated with the discovery of an iridium anomaly at the Cretaceous-

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Tertiary boundary and its implications for their cause (ALVAREZ et al., 1980). The effects of mass extinctions include marked changes in the composition and diversity of the world biota and in the structure and integrity of various fossil communities. Because of the relatively abrupt nature of some mass extinctions, they have become the bases for recognizing chronostratigraphic boundaries or intervals at the era, system, series and stage levels. Unlike most recent studies of mass extinction that have focused on documenting either their effects on particular higher taxa, their precise timing to estimate rates of extinction, their biogeographic scope or their causes, this paper deals only with the effects of extinction and the recovery of fossil reef communities.

The three extinctions marking Middle-Late Devonian stage boundaries (end-Givetian; end-Frasnian; end-Famennian) differ from mass extinctions by their sequential and cumulative effects. For example, in the initial analysis by RAUP & SEPKOSKI (1982, Fig. 1) of rates of family level extinction, none of the Devonian extinctions was statistically different from normal or background extinction rates but when they examined the effects of extinction and origination rates on global standing diversity (their Fig. 2), the end-Frasnian extinction was of comparable intensity to four of the five more typical mass extinctions and therefore may be regarded as a true mass extinction event. Re-investigation of up-dated family-level diversity, origination and extinction data (SEPKOSKI, 1993) suggest that the end-Famennian event was also comparable to the end-Frasnian event and has also been termed a mass extinction (WANG et al., 1993).

The effects of the Devonian extinctions on reef communities are of special importance but are masked to some degree in the RAUP & SEPKOSKI (1982) and SEPKOSKI (1993) analyses for two reasons: 1) their data base excluded calcareous algae which were of major importance in reef communities and 2) they were not as abrupt as more typical mass extinctions (JOACHIMSKI & BUGGISCH, 1993). Nonetheless, previous authors (McLAREN, 1982; McGHEE, 1982, 1989; JOACHIMSKI & BUGGISCH, 1993) have noted the considerable effect of the extinctions on reef communities.

1.2 Reef-building guilds

FAGERSTROM (1987) subdivided the ecologic/paleoecologic structure of reef communities into five guilds of which only three (Constructor, Binder, Baffler) are responsible for the building of reefs. Members of the Destroyer Guild subvert the building process by breaking down the reef framework and the Dweller Guild plays a passive role with regard to the building vs. destruction processes. Determination of reef guild structure requires two steps (FAGERSTROM, 1988):

1. assignment of individual organisms or colonies to a particular guild using a hierarchical group of criteria (FAGERSTROM, 1991).

2. determination of the degree of guild overlap among the reef-building guilds based on skeletal size and packing density of the members of each guild.

The guild concept (ROOT, 1967) is particularly well-

sued to the study of high diversity communities such as reefs with high preservation potential of the most abundant taxa. In such communities, niche and trophic structures are much too complex for analysis. Additional to the advantages cited by FAGERSTROM (1988, 1991), the reef guild concept is shown here to be of particular value for study of the effects of extinction events on the paleoecologic structure and functional aspects of fossil reef communities and on the reef limestone biofacies produced by these communities.

This study is a paleoecological analysis of each of the three major aspects of modern and fossil community organization: taxonomic composition and diversity (KAUFFMAN & FAGERSTROM, 1993) and paleoecologic structure. It will emphasize four selected, but "typical" reef frame-building communities (one Frasnian, two Famennian, one Viséan) and one mud mound-building community (Tournaisian) spanning the pre-extinction, extinction and recovery phases of this history.

1.3 Reef biofacies

It is the reef-building guilds (i.e. Constructor, Baffler, Binder) that distinguish reef communities from all others; in typical modern and ancient reefs they provide the rigid framework, large skeletons, topographic relief and enhance the deposition of internal sediment (FAGERSTROM, 1987, p. 3-15). However, there is considerable variation among these distinguishing features; stromatolitic reefs, mud mounds and modern *Halimeda* banks/bioherms (eg. ORME & SALAMA, 1988; MARSHALL & DAVIES, 1988) differ significantly from more typical reefs by their lack of a rigid skeletal framework. Nonetheless, they are also amenable to application of the reef guild concept for analysis of their paleoecologic structure (see FAGERSTROM, 1987, p. 268-272 and below).

The reef-building guilds may be depicted as the ecological end-members (corners, Fig. 1A) of reef communities. Because members of the Constructor and Binder Guilds usually have very high preservation potentials, framework reefs are also more common features of carbonate rocks than stromatolite reefs and mud mounds. The preservation potential of bafflers varies from good (*Halimeda*; stalked Crinoidea) to poor (frondescent brown algae) making communities dominated by this guild considerably more difficult to interpret (EMBRY & KLOVAN, 1971).

Each reef-building guild is reflected in major petrographic features of reef limestones (FAGERSTROM, 1985, 1987), i.e. the reef guild concept provides a link between the functional aspects of reef paleoecology and the petrographic classification of reef carbonates (corner areas, Fig. 1A) based on the relative importance of members of each guild. Thus, the commonly used petrographic terms for reef carbonates (framestone, boundstone, bafflestone) are biofacies that recognize the dominant influence of the Constructor, Binder and Baffler guilds respectively, in the original living reef community.

There is no separate term for either communities or biofacies in which the reef-building guilds are of similar overall importance, i.e. balanced reef communities

Fig. 1A. Ternary diagram showing the three reef-building guilds as end-members (corners), and idealized distribution of biofacies (framestone, boundstone, bafflestone) relative to the dominance of particular guilds and the uniform importance of these guilds in balanced reef communities.

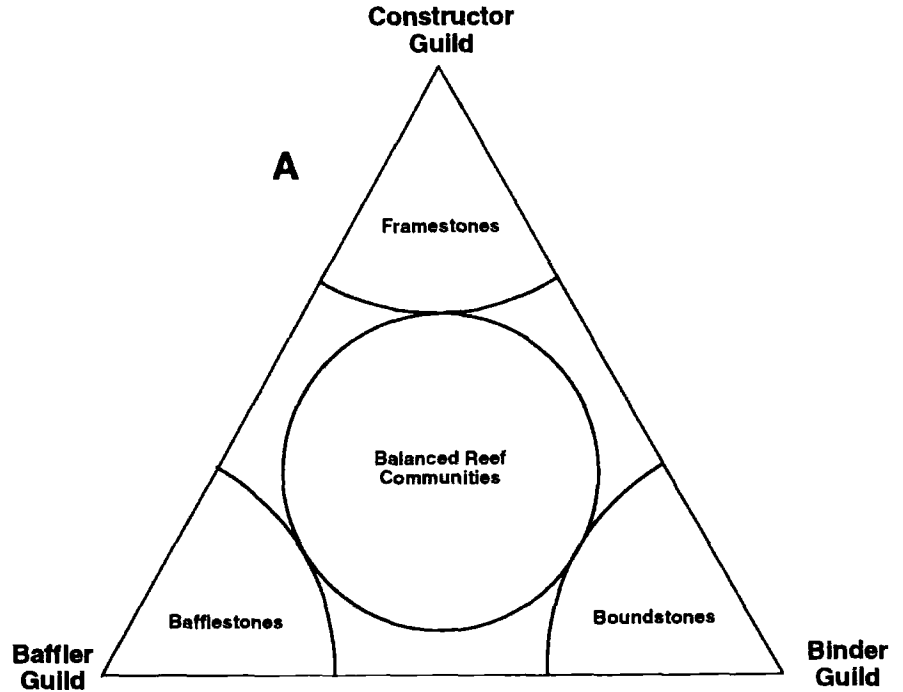
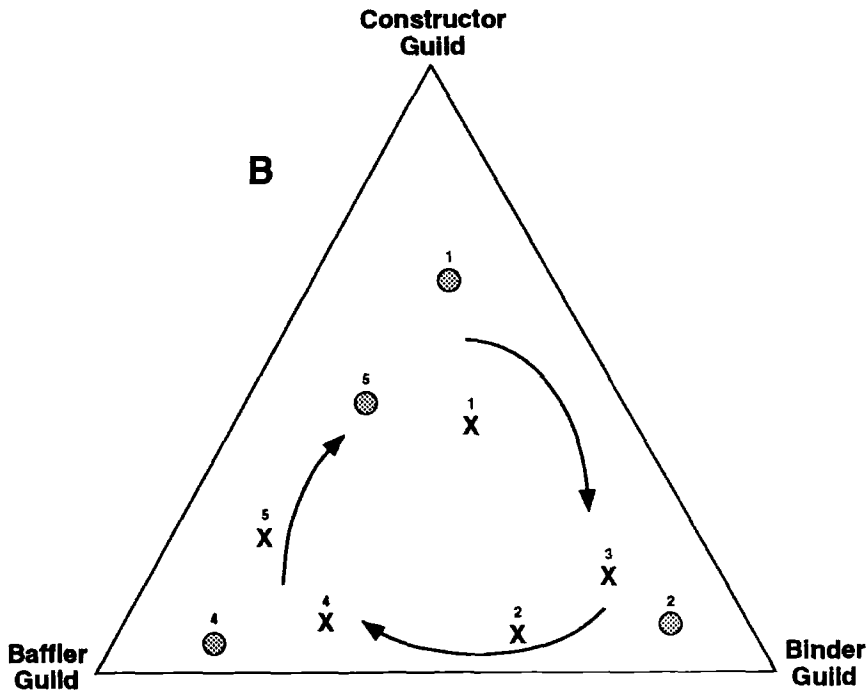


Fig. 1B. Ternary diagram of Frasnian, Famennian, Tournaisian and Viséan communities discussed in text

- 1= Frasnian, Canning Basin, Australia;
 - 2= Famennian, Canning Basin;
 - 3= Famennian, Alberta Basin, Canada;
 - 4= Tournaisian, Dinant Basin, Belgium;
 - 5= Viséan, lower Akiyoshi Limestone, Honshu Island, Japan
- showing relative importance of each reef- or mound-building guild in the overall structure and biofacies. X's mark locations based on diversity data in Table 1; shaded circles



indicate locations based on author's estimate of the volumetric importance of each guild based on field observations and published data (see text). The location of the X for the Tournaisian (4) based on assignment of *Amplexus* to Constructor Guild; if it is rare (a dweller) the X would fall on the base line of the diagram. Numbers (1-5) and arrows show the temporal sequence and evolution of guild structure and resulting biofacies in response to two Devonian extinction events (end-Frasnian, end-Famennian) and the recovery of reef- or mound-building communities during the Tournaisian and Viséan.

(Fig. 1A). Existing petrographic terminology emphasizes local areas, commonly based on hand specimens or thin-sections (cf. NAGY, 1985), dominated by one (eg. bafflestone) or two (eg. boundstone-bafflestone) guilds (FAGERSTROM, 1987, Pls. 7, 8, 20b, 23b). Conversely, the intention here is to determine the relative importance (genus/species diversity; abundance) of each reef-building guild in the overall paleoecological structure of each community as discussed below.

2 MIDDLE-LATE DEVONIAN REEF COMMUNITIES

2.1 Pre- Frasnian

The general nature (composition, diversity, structure) and evolution of mid-Paleozoic (Middle Ordovician-Frasnian) and late-Paleozoic (Famennian-Permian) reef communities has been compared and summarized by FAGERSTROM (1987). He concluded that there was an overall

similarity and general stability in the composition and guild structure among mid-Paleozoic communities during this extended period (100+ Ma). The same frame-building higher taxa (stromatoporoids, rugose and tabulate corals, algae) dominated most communities and origination and extinction rates of genera and species appear to have been at normal or background rates. Compared to the common small, interior shelf-craton mid-Paleozoic reefs, many Frasnian and a few in the Famennian are large shelf margin reefs, with clearly defined crest, back- and fore-reef divisions. Well-known examples, discussed below, include reefs marginal to the Canning Basin, Western Australia, the Alberta Basin, western Canada and the Dinant Basin, Belgium.

Devonian genus/species richness peaks for both rugose corals and stromatoporoids were in the Eifelian-Givetian (SORAUF, 1989; STEARN, 1982) and for higher taxa of calcareous algae the Paleozoic peak was in the Carboniferous (CHUVASHOV & RIDING, 1984, Fig. 1; ROUX, 1985, Fig. 39; FAGERSTROM, 1987, Fig. 7-1). However, for "reef-forming" calcareous algae the Paleozoic diversity peak was Devonian (CHUVASHOV & RIDING, 1984, Fig. 8). Thus, the stage was set in the Givetian for major extinction-induced reorganizations of reef communities during the Late Devonian-Early Carboniferous.

2.2 A Frasnian reef community, Australia

The reefs of the Canning Basin are of special importance because they are taxonomically diverse and conformably span the Frasnian-Famennian boundary (PLAYFORD et al., 1984). The general composition (higher taxa) and lateral distribution of the reef, fore- and back-reef biota are reviewed in PLAYFORD et al. (1976), PLAYFORD (1980) and PLAYFORD & COCKBAIN (1989). Species-level systematic monographs have been completed on the frame-building calcareous algae (WRAY, 1967), stromatoporoids (COCKBAIN, 1984) and corals (HILL & JELL, 1970). In the following discussion, only those species occurring in the "reef margin, reef, reef flat, marginal slope or platform margin facies/subfacies" of PLAYFORD & COCKBAIN (1989) are included. For the Frasnian they consist of the Sadler and Pillara Limestones and for the Famennian the Windjana Limestone.

Appendices 1-3 indicate the guild to which each algal, stromatoporoid and coral species is assigned and their stratigraphic occurrences. Although non-stromatoporoid sponges are moderately diverse (7 spp. in the Sadler; none in the Pillara; 2 spp. in the Windjana) and because most specimens are small and have undergone pre-burial transportation they are assigned to the Dweller Guild (RIGBY, 1986, p. 5, Table 1; cf. Playford, 1980, p. 826). Conversely, most of the algae, stromatoporoids and corals are either in growth position or are *in situ* (EMBRY & KLOVAN, 1971; i.e. have undergone minimal transportation within their life habitat).

Although WRAY (1967) described fourteen species (excluding *Keega australe*, a stromatoporoid) of calcareous algae from the Canning Basin, only five species, plus the stromatolites are of significant volumetric importance. Five

others (including *Frutexitis* sp.) are also regarded here as "reef-building" (Appendix 1); the remaining species were reef dwellers. The composition and functional roles of this microflora and those in the Dinant and Alberta Basins, Belgium and Canada are remarkably similar (WRAY & PLAYFORD, 1970; WRAY, 1972; TSIEN, 1979). In the Canning Basin, nearly all of the reef-building species are present in both Frasnian and Famennian rocks. However, during the Frasnian the algae are volumetrically subordinate to both the stromatoporoids and corals in most sectors of the reef tract.

Of the 24 Frasnian stromatoporoid species described by COCKBAIN (1984, Fig. 6), four species are absent from the reef margin and two species (*Atelodictyon stelliferum*, *Dendrostroma oculatum*) are here assigned to the Dweller Guild because of their low skeletal volume in the reef framework. Because of their probable morphologic plasticity, two or three species can be assigned to membership in two guilds and five other species assigned to either the Baffler or Binder Guild appear to be so abundant and to have such great skeletal volume (COCKBAIN, 1986, Fig. 6) that they also overlap the Constructor Guild (Appendix 2). These data confirm the author's field observations in the Canning Basin where he estimated that stromatoporoids, either in growth position or *in situ*, contributed the greatest skeletal volume to the reef framework (eg. coenostea of the Constructor-Binder Guilds are large [1+m in diameter], domal-hemispherical-laminar, densely packed, locally of greater volume than the matrix). The Baffler Guild includes current-aligned fragments of dendroidal *Amphipora/Stachyodes* coenostea, locally of greater volume than the matrix; FAGERSTROM, 1987, Pl. 41b). Previous authors (PLAYFORD & LOWRY, 1966; PLAYFORD, et al., 1976; FAGERSTROM, 1987, p. 361-362, Pl. 28) have noted the close association (encrusting, overtopping, inter-fingering) between various algae, especially stromatolites, *Renalcis* (Binder Guild) and *Sphaerocodium* (Baffler Guild), and tabular (Binder Guild)-dendroidal (Baffler Guild)-domal (Constructor Guild) stromatoporoids. These associations were very important for enhancing the topographic relief and rigidity of the framework. Similarly close associations between algae and corals are much less common.

Although the data for skeletal shape, size and packing density for the rugose corals are not as complete (HILL & JELL, 1970) as those for the stromatoporoids, they can be also assigned to guilds (Appendix 3). One species (*Catactotoechus irregularis*), assigned to the Dweller Guild, may be sufficiently abundant locally to overlap the Constructor Guild and two other species appear to be morphologically plastic and thus may be members of more than one guild.

John Jell (personal communication, 1991) indicated that the disphyllids are the largest coralla with branches pointed toward the basin (into the surf as possible analogs of *Acropora palmata* in modern western Atlantic reefs) and that the coralla of *Hexagonaria playfordi* and *Argutastrea hullensis* are much smaller (almost "button-shaped") and contribute a relatively small volume to the framework (cf. PLAYFORD & LOWRY, 1966, p. 46; FAGERSTROM, 1987, Table 12.8).

In summary, the data of Appendices 1-3 and Table 1 indicate the highest overall diversity is in the Constructor

Guilds; Higher Taxa	Frasnian Canning Basin (Species Diversity)	Famennian Canning Basin (Estimated Species Diversity)	Alberta Basin (Estimated Species Diversity)	Tournaisian Dinant Basin (Estimated Species Diversity)	Visean S. Honshu Island
I. Constructor					
Stromatoporoida	7	1	1	0	0
Rugosa	12	0	0	1?	3
Tabulata	2	0	0	0	0
	----	---	---	---	---
Intra-Guild Totals	21	1	1	1?	3
II. Binder					
Algae/stromatolites	6	6	+	2?	+
Stromatoporoida	6	1	3	0	0
Tabulata	5	2	0	0	0
Bryozoa	?	?	0	1	1
	----	---	---	---	---
Intra-Guild Totals	17?	9?	4?	3?	2?
III. Baffler					
Algae/stromatolites	4	4	0	0	+
Stromatoporoida/ other sponges	5	0	1	+	0
Tabulata	2	0	0	0	0
Bryozoa	?	+	0	6?	7?
Pelmatozoa	+	?	?	++	+
	----	---	---	---	---
Intra-Guild Totals	12?	5?	1?	8?	9?
BUILDING-GUILD TOTALS (approx.)	50	16	6	12	14

Tab. 1. Minimum diversity in reef-building guilds (based on Appendices 1-4). Data for the Alberta (STEARNS, 1988) and Dinant Basins and Honshu (FAGERSTROM, 1987, p. 374-376) not directly comparable to Canning Basin (see text). + = present; ++ abundant; diversity uncertain. Diversities in Albert and Dinant Basins and Honshu Island not directly comparable to Canning Basin (see text).

Guild with somewhat lower diversities in the Baffler and Binder Guilds. Furthermore, the presence of large, well-skeletonized stromatoporoids and colonial corals, morphological plasticity and dense packing with guild overlap among the stromatoporoids and corals clearly indicate the predominant volumetric importance of the Constructor Guild during the Frasnian. However, diversity in the reef-building guilds was balanced (Fig. 1B).

As in most other large reef tracts, there are important local variations: 1) large volumes of the reef crest limestone are framestones (*sensu* EMBRY & KLOVAN, 1971) but upper marginal/seaward slopes consist largely of skeletal boundstone where gravity-induced transport of intraclasts was reduced by the Binder Guild; 2) deeper water stromatolite boundstones are locally important as near Elimberrie Spring (PLAYFORD et al., 1976) and 3) *Amphipora-Stachyodes* dominated bafflestones are widespread on the reef-flat (PLAYFORD & COCKBAIN, 1989) as are local sponge bafflestones (RIGBY, 1986, p.5).

2.3 Effects of Frasnian-Famennian extinction, Australia

Subsequent to the Frasnian-Famennian extinction event, reef-building continued unabated in northwestern Australia.

Famennian reefs are nearly as large as those of the Frasnian and are located in the same general areas. However, except for the algae, there were drastic changes in the composition, diversity and guild structure of Famennian reefs compared to those of the Frasnian (Table 1; Fig. 1B).

The same five algal species of greatest importance in building Frasnian reefs became the only builders of Famennian reefs (Appendix 1). Of the algal builders, *Girvanella wetheredi* became extinct at the end of the Frasnian and *G. ducii* first appeared in these reefs during the Famennian. In the reef-building guilds, Famennian algae increased enormously in their volumetric importance relative to the Frasnian and assumed most of the functional roles of the Frasnian stromatoporoids and corals (Appendix 3), a type of ecological replacement. Locally, *Renalcis* spp., stromatolites and *Sphaerocodium* spp. (Frasnian binders-bafflers) so completely dominated Famennian reef-building communities that they assumed the constructional role by guild overlap (FAGERSTROM, 1987, Pls. 27, 28).

The most significant taxonomic difference between the Frasnian and Famennian Canning Basin reef communities involved the stromatoporoids. Although elsewhere several stromatoporoid genera/species survived the Frasnian-Famennian extinction event (STEARNS, 1987; STEARNS et al., 1987, Table 2; COCKBAIN, 1989, Table 2), none survived it in

northwest Australia (COCKBAIN, 1989, Table 1). However, the Famennian reefs in the Canning Basin do contain two stromatoporoid species, both absent from the Frasnian (Appendix 2). In addition to this drastic reduction in species diversity, coenostea of Canning Basin Famennian stromatoporoids are much less abundant and smaller than those of the Frasnian; only one species was frame-building (Appendix 2).

The effect of the Frasnian-Famennian extinction event on the diversity and abundance of Canning Basin reef-building corals (Appendix 3) was nearly as drastic as it was on stromatoporoids. Famennian reefs contain only about four coral species and only one (*Alveolites suborbicularis*) was a frame-builder. HILL & JELL (1970) did not provide adequate information to assess the importance of guild overlap among the other coral species.

The reef-building species that survived the Frasnian-Famennian mass extinction event in the Canning Basin consist of eight algae (including stromatolites) and only 1-2 corals (Table 1). This high taxonomic turnover of the reef-building stromatoporoids and corals at the Frasnian-Famennian boundary is even greater than the turnover of either level-bottom or pelagic taxa that has been so clearly documented elsewhere by previous authors (e.g. McLAREN, 1970, 1982, 1983; LARWOOD, 1988; MCGHEE, 1982, 1989; SANDBERG et al., 1988). Furthermore, there was an equally drastic change in structure and biofacies from communities with a balanced reef-building guild structure in the Frasnian to reefs dominated by the Binder Guild in the Famennian (Fig. 1B) forming boundstones. Thus, in terms of their guild structure, Famennian communities are analogs of algal ridge communities in modern Pacific reefs.

2.4 The last Devonian reef community?

A mid-Famennian stromatoporoid-built reef is present in the subsurface near Normandville, Alberta, Canada and provides an important taxonomic contrast to the Famennian reefs in the Canning Basin (Table 1). (The precise age of the youngest reefs in the Canning Basin is uncertain [COCKBAIN, 1989]; some may also be mid-Famennian). The Normandville reef and adjacent facies are known only from cores, and thus provide much more limited sampling than from outcropping reefs and therefore diversity data for the Alberta Basin (Table 1) are not directly comparable to those from the extensive outcrops in the Canning Basin. Nonetheless, the general composition (STEARNS et al., 1987; STEARNS, 1988) and guild structure of the community can be partially reconstructed. Five species of stromatoporoids were the chief frame-builders (Appendix 2). Their coenostea comprise 5-15% of the reef volume and most are laminar/tabular (Binder Guild), producing a boundstone reef (Fig. 1B). Other coenostea are less abundant but they include hemispherical constructors perhaps forming local framestones. Thin layers of unidentified algae encrust (Binder Guild) the upper surfaces of some coenostea and current-baffling crinoids were also present in the community. Corals apparently were absent or rare, as in the Canning Basin Famennian.

2.4.1 The end-Famennian reef extinction event

Some compilations of Phanerozoic mass extinctions fail to show the complete demise of reef communities during the mid-late Famennian (eg. RAUP & SEPKOSKI, 1982). Conversely, Figures 3, 4 and 6 in SEPKOSKI (1993) indicate an important global end-Famennian extinction. Extinction of framework reefs at this time is largely due to the extinction or reduced abundance of reef-building calcareous algae, major elements of Famennian reefs that were excluded in Sepkoski's compilation. In addition, discrepancies in the range zones and/or abundances of such reef-building algae as *Renalcis*, *Epiphyton/Paraepiphyton*, *Sphaerocodium/Rothpletzella*, *Girvanella*, *Solenopora/Pseudosolenopora* and *Parachaetetes* between CHUVASHOV & RIDING (1984, Figs. 3, 4) and MAMET (1991, Figs. 2, 3) tend to confuse the taxonomic impact of an end-Famennian extinction. Nonetheless, for reefs the extinction of algae was real and fatal.

Conversely, the diversity of non-reef algae does not reflect an end-Famennian extinction event (cf. CHUVASHOV & RIDING, 1984, Fig. 1; ROUX, 1985, Fig. 39). Of the nearly 50 genera of Famennian-Tournaisian calcareous algae (MAMET, 1991, Figs. 2, 3) none became extinct at the end of the Famennian, 40 crossed the boundary unchanged in their abundance, four genera increased in abundance and three genera arose in the Tournaisian.

STEARNS (1987), STEARNS et al. (1987) and COCKBAIN (1989) have reviewed the nature and occurrence of Famennian stromatoporoids, reefs and reef-like rocks. The latest Famennian rocks (including "Strunian" in the Ardennes Mountains) contain a greater diversity of stromatoporoids than the underlying Famennian but specimens are small and rare. Many species belong to the primitive and long-ranging Order Labechiida (STEARNS, 1993, Text-fig. 4) which was of limited importance in reef communities, except during the Middle Ordovician (KAPP, 1975; KAPP & STEARNS, 1975) and in the Normandville reef (see above). These authors concluded that the diversity, geographic distribution and reef-building *potential* of latest Famennian stromatoporoids was much greater than commonly assumed. However, the end-Famennian extinction of all Paleozoic stromatoporoids and nearly all rugose coral species (POTY, 1989; CONIL et al., 1990) and some Tabulata (another *potential* reef-builder) was a minor aspect of reef extinction; Devonian reef-building had ceased by the mid-Famennian, except possibly in the Omolon region (SHILO et al., 1984). None of the Tabulata or calcareous algae that survived the end-Famennian extinction were builders of either latest Famennian or Tournaisian framework reefs.

2.5 Extinction of Devonian reef communities: summary

2.5.1 Reef communities were different

Although most reef communities appear to have greater species diversities than adjacent level-bottom and pelagic communities (cf. BAMBACH, 1977; KAUFFMAN & FAGERSTROM, 1993), reef diversity is commonly concentrated in the Dweller Guild rather than in the reef-building guilds (FAGERSTROM,

1987). However, species diversity is not the only, or even the best measure of the reef-building potential of a benthic community; many modern and ancient reefs were built by a surprisingly few species (FAGERSTROM, 1987; KAUFFMAN & FAGERSTROM, 1993). Thus, for typical reef communities it is large skeletal size and high packing density of the constructors and/or binders that make them unique; members of the Baffler Guild do not build "true" framework reefs by themselves (see below).

The main reason for the failure of the Devonian extinction of reef-building taxa to appear as a mass extinction event in the RAUP & SEPkosKI (1982) compilation is because reef extinction history was a prolonged (approx. 25 Ma) successional interval. It involved the cumulative phylogenetic and ecologic effects of family-, genus- and species-level excesses of extinctions over originations. This extinction produced a slow but progressive decrease in the diversity of reef-building taxa that began in the Eifelian-Givetian and was not completed until the end of the Famennian. It had one major peak (end-Frasnian; generally regarded as a mass extinction) and two minor peaks (end-Givetian; end-Famennian).

The end-Frasnian event is clearly shown in the Canning Basin building-guild diversity data of Table 1 but the table indicates only a moderate diversity decrease from the mid-late Famennian to the Tournaisian. However, this shift in composition, skeletal strength/rigidity and skeletal size produced a shift from predominantly framework reefs in the Devonian to frameless "mud mounds/reefs/banks" in the Tournaisian.

The Devonian extinctions were cumulative in two ways: 1) no single episode or higher taxon accounts for the full impact on reef communities and 2) the excesses of extinctions over originations was progressive resulting in a slow diminution of reef-building taxonomic diversity from the Eifelian to the Famennian. Newly evolved taxa failed to replenish the taxonomically depleted reef-building guilds nor were their skeletons sufficiently large or densely packed to become reef-builders by guild overlap. Thus, the final demise of Devonian reefs in the mid-late Famennian appears to have slightly pre-dated the final extinction of many potential reef-building higher taxa that had been the chief reef-builders during the preceding 115+ Ma.

2.5.2 Taxonomic summary

A review of the Devonian-Carboniferous histories of the major reef-building higher taxa will clarify the progressive aspect of this extended extinction interval (Table 1):

1. Corals

The effect on the Rugosa, the best documented Devonian higher taxon, is due to a succession of detailed studies by OLIVER & PEDDER (1979), SORAUF & PEDDER (1986) and SORAUF (1989). These authors separated the histories of the shelf-dwelling from the basinal/deeper water taxa and the solitary from the colonial taxa and found that the effects of origination and extinction on these groups and on reef

history were quite different. The critical compilations so far as reef-building taxa are concerned are those of SORAUF (1989, Figs. 1, 8, 9-13).

The progression is well-shown by the generic diversity (Figs. 8-10), origination (Fig. 9) and extinction (Fig. 12) totals for the colonial shelf-dwelling (potential reef-building) Rugosa. They decreased in generic diversity from an Eifelian maximum (110 genera) to a Famennian minimum (2 genera) with the steepest drop occurring at the Frasnian-Famennian boundary (Figs. 1, 13); Figs. 11, 12 indicate a lesser extinction at the end of the Givetian (Figs. from SORAUF 1989).

Although there is some disagreement on the precise location of the Famennian/Strunian-Tournaisian boundary in the Dinant Basin, these general aspects of an end-Famennian extinction are confirmed by the detailed analyses of rugosan range zones by POTY (1984, 1989; CONIL, et al., 1990). No genera or species of Strunian Rugosa cross the boundary (RC 0 to RC 1) and every Tournaisian rugosan genus and species is absent from the Strunian, i.e. the turnover (extinctions plus originations) is 100%. Conversely, each of the three Strunian tabulate corals in this basin (CONIL, et al., 1990) also occurs in the Tournaisian, i.e. there is no turnover.

2. Stromatoporoidea

Although the genus- and species-level taxonomy of Devonian stromatoporoids is not as firmly established as for corals, the compilations of STEARN (1982; 1993, Text-Fig. 4) and COCKBAIN (1989) clearly indicate a progressive decline in stromatoporoid diversity from a Givetian maximum with a major extinction at the end of the Frasnian, a lesser extinction at the end-Givetian and final extinction at the end of the Famennian/Strunian. In the Dinant Basin the extinction of Paleozoic stromatoporoids approximately coincides with the Famennian-Tournaisian turnover of rugose corals (POTY, 1989).

3. Calcareous algae

The Devonian-Carboniferous history (diversity, stratigraphic range, abundance) of reef-building calcareous algae is even less certain than that of the stromatoporoids. However, it contrasts sharply with the histories of both the corals and stromatoporoids. There is a general similarity in the composition and generic diversity of reef-building calcareous algae from the Ordovician through the Famennian (CHUVASHOV & RIDING, 1984, Figs. 3, 4); all genera survived the stromatoporoid-coral extinction events at the end of the Givetian and Frasnian. However, of the eight "groups" of Famennian reef-building algae recognized by CHUVASHOV & RIDING, (1984, Figs. 3, 4), six became extinct at the end of the Strunian (but did not build Strunian reefs) and the other two did not survive the end of the Tournaisian. The compilation of MAMET (1991, Fig. 3) indicates that *Renalcis*, the chief Frasnian-Famennian reef-builder in the Canning Basin, survived the end-Famennian extinction but was rare until its extinction in the Late Carboniferous.

The progressive Devonian extinction differs significantly in its duration and cumulative effect on reef communities from the three mass extinction types described by

KAUFFMAN (1988): catastrophic, step-wise and graded. The approximately 25 My from the Eifelian-Givetian maxima in stromatoporoid, coral and crinoid (UBAGHS et al., 1978) diversities to their Late Famennian minima exceeds by about an order of magnitude, the duration of Kauffman's step-wise and graded types (both 1-3.5 My) and is almost infinitely longer than his catastrophic extinction (i.e. days to weeks/months).

3. Tournaisian Mud Mounds: Baffler-Binder Guild Communities

3.1 General aspects

The Tournaisian represents the nadir in mid-late Paleozoic reef development; globally there are no framework reefs of this age. The succession of Devonian extinctions removed nearly all taxa living in shallow water that previously were important in frame-building and no surviving or new taxa took their places. Conversely, the Tournaisian represents the zenith in abundance and size of non-framework mud mounds (also called banks, build-ups, reefs). These structures are characterized as over-thickened, massive (unbedded to poorly bedded), mud-, bryozoan- and crinoid-rich carbonate rocks with poor- to well-defined cores giving them an external form similar to framework reefs and margins commonly marked by steeply dipping (up to 50°) flank beds.

The most thorough studies of Tournaisian mud mounds are those of LEES and his collaborators (eg. LEES, 1964; LEES et al., 1977; LEES, 1982; LEES, HALLET & HIBO, 1985; LEES & MILLER, 1985, and paper in press) on those in western Europe, with emphasis on the mounds in the Dinant Basin, called Waulsortian. In Belgium, Waulsortian mud mounds are confined to the mid-Tournaisian and lower Viséan stages. Although similarly mud-rich, frameless, over-thickened mounds occur in Middle Ordovician rocks of Nevada (ROSS et al., 1975), the Frasnian-Famennian in Belgium and northern France (BOULVAIN & COEN-AUBERT, 1989; TERMIER et al., 1989; DREESEN et al., 1985) and elsewhere in Lower Carboniferous rocks (WILSON, 1975, p. 148-168; BOLTON et al., 1982; LEES & MILLER, in press) the present discussion is confined to those of Tournaisian age.

3.2 Origin(s)

The origin(s) of the Waulsortian mounds has been controversial almost continuously since their original description (DUPONT, 1863; LEES, 1988). Central to these discussions are three major problems: a.) What was the source(s) of the very large volume of mud/micrite compared to the thinner, adjacent and contemporaneous rocks? Was the mud autochthonous or allochthonous? Was it of organic or physical-chemical origin?; b.) Why was the mud retained on the mounds and steeply dipping flanks rather than being shed to the adjacent inter-mound areas?; and c.) What were the ecologic-sedimentologic functions of the various organisms inhabiting the mounds, many of which were members of enigmatic/problematic taxa?

3.3 The mound-building biota was different

The Waulsortian mound-building biota present in Phases A-C of LEES & MILLER (1985) may be more diverse at both high and low taxonomic levels than those of Famennian and Viséan framework reefs (Tournaisian species diversity in Appendix 4 is uncertain but low due to poor preservation and lack of modern taxonomic monographs on the bryozoa and pelmatozoans). From the guild viewpoint, the most important difference between Tournaisian mud mound communities and Famennian and Viséan reef communities is the absence of frame-building stromatoporoids and colonial Rugosa in the Tournaisian. Although other potential frame-builders such as algae (*Girvanella*; other filamentous forms?) and relatively large, solitary Rugosa are present (Appendix 4), their skeletal size and/or packing densities were insufficient to produce framework reefs. Furthermore, none of the 50 pre-Tournaisian non-reef algal genera that were also present in the Tournaisian (discussed above), shifted their preferred habitat to the mud mounds nor did they participate in mound-building.

The dominant skeletal macro-invertebrates in the mounds are fenestrate Bryozoa and crinoids which commonly are sympatric but they also occur allopatrically. Several workers (e.g. PRAY, 1958; LANE, 1971; FAGERSTROM, 1987; MCKINNEY et al., 1987) have discussed the roles of these organisms in the origin of the mounds and generally agreed that their erect growth habit and cylindrical or fan-like growth forms may have performed the function of current baffling to produce a leeward zone of low turbulence from which suspended mud was deposited. However, other authors (LEES, 1964; LEES & MILLER, 1985, and paper in press; TSIEN, 1985) have raised serious objections to the baffling hypothesis and minimized the importance of the baffling role of the fenestrates and crinoids for sediment deposition.

The present discussion, emphasizing the biota and its functional roles, is intended to suggest modifications to previous and current interpretations rather than a final solution to the "Waulsortian dilemma." The Tournaisian biota was unique in several ways when compared to those of other Late Devonian-Early Carboniferous stages:

1. The Tournaisian was a time of rapid evolutionary diversification among the fenestrate bryozoans (MCKINNEY & JACKSON, 1989, Fig. 1.14) and pelmatozoans (MOORE, 1955, Fig. 4; UBAGHS et al., 1978) that survived the Devonian extinctions and both groups attained their late Paleozoic acmes in diversity and abundance during the Early Carboniferous. Although neither detailed mapping of skeletal fragments (eg. LANE, 1971, Fig. 6), nor statistical comparisons of the densities of fenestrate and crinoid fragments in the Waulsortian mounds relative to the inter-mound areas have been done, these taxa as well as others assigned to the Dweller Guild (eg. brachiopods, ostracods), appear to have lived on the mounds (*in situ* skeletons of EMBRY & KLOVAN, 1971), i.e. their abundance in the mounds does not represent accumulations of transported skeletal fragments from inter-mound habitats (MCKINNEY et al., 1987). Supporting evidence includes the decreasing ratio of smaller fragments to larger fenestrate fronds/sheets from the lower parts of the

flanks to the mound summits (LEES & MILLER, in press). However, an undetermined proportion of the fenestellid and encrinal "hash" found in pockets and layers may represent breakage during soft sediment compaction.

Because fenestrate bryozoans are abundant, their roles in sedimentation are critical for understanding mound origin. They were important in mound paleoecology and sedimentology because: 1) the actively feeding zooids probably created local currents of greater velocity than the ambient currents; both local and ambient currents provided access to suspended food and induced sediment deposition leeward of the zoarium (McKINNEY et al., 1987; McKINNEY & JACKSON, 1989) and 2) the erect growth habit and fan-shape of the zoaria reduced ambient current velocities to passively enhance sediment deposition. These same adaptations for suspension feeding and enhancement of sedimentation are also attributable to the crinoids and perhaps even to the hyalostellid sponges (Appendix 4). Thus, the combination of rapid Tournaisian evolutionary diversification and increased abundance of the dominant skeletal macro-invertebrates, their erect growth habits and suspension feeding activities provided a variety of biologically mediated mechanisms for enhanced sediment deposition on the mound surfaces.

2. Other survivors of Devonian extinctions that were important in the Tournaisian mounds include enigmatic structures variously called *Stromaiaocus*, *Ptylostroma* or *Stromatactis*. The organic vs. inorganic origin of these peculiar structures has been disputed for decades (eg. LEES, 1964; HECKEL, 1972; BECHSTÄDT, 1974; MONTY, 1982; TSIEN, 1985a, 1990; BATHURST, 1959, 1980, 1982). If they were organic, their taxonomic affinities, ancestors-descendants, adaptations for surviving extinction (i.e. possible "different-rules" taxa of GOULD [1989, p. 305-308]) and function(s) in mound communities are also unknown.

3. The enormous turnover in the diversity, composition and structure of reef and level-bottom communities resulting from the Givetian-Famennian extinctions may have produced an evolutionary-ecological "release" from the constraints of competition in the Tournaisian. The Devonian extinctions may have opened new evolutionary paths for the survivors ("different rules" taxa?) as well as newly evolved organisms of uncertain biological affinities that were members of the mud mound communities. They include the moravamminids, aoujgaliids (TERMIER et al., 1977), salebrids, *Globochaete*, *Sphaerinvia* and possible algae (LEES & MILLER, 1985, in press; RIDING, 1977). In addition, the habitat(s), importance and function(s) of *Girvanella* (RIDING, 1975; CHRISTOPHER, 1990) and stromatolites/cryptalgae (PRATT, 1982) in mound-building relative to better skeletonized taxa are also uncertain.

4. The apparent low biomass of mound-living skeletal binders/encrusters and grazers/destroyers opened the substrate to colonization by various organic filaments, mats and gelatinous/mucus/bacterial sheets and "biofilms" (PRATT, 1982; LEES & MILLER, in press) to trap and stabilize mud and skeletons on the summits and flanks of the mounds.

5. Although there are several potential sources of the mound carbonate mud, those that are biological rather than physical-chemical appear to be the more probable (TSIEN,

1985b; LEES & MILLER, in press), especially if the water depths (220-300+m; at-below the thermocline?) indicated by LEES et al. (1985) and LEES & MILLER (1985, in press) are correct (but see below). The Early Carboniferous algal forms (CHUVASHOV & RIDING, 1984; MAMET, 1991) also may have included taxa analogous to living soft-bodied codiaceans such as *Penicillus*, *Rhipocephalus* and *Udotea* that were capable of producing large volumes of aragonite needles/mud as in modern mud mounds (STOCKMAN et al., 1967; FAGERSTROM, 1987, p. 129).

In summary, the Tournaisian mound-building biotas differed from the reef-building guilds of the Devonian and Viséan by: 1) the near absence of taxa with large, rigid skeletons, 2) the abundance of diverse, weakly skeletonized, erect, suspension-feeding, sediment-baffling bryozoa and crinoids, 3) the presence of numerous taxa of uncertain biological affinities and ecological functions and 4) the likely presence of various non-skeletal taxa that were potential sediment trappers/stabilizers and mud-producers.

3.4 Mound-building guilds and biofacies: conclusions

"The ingredients for recognition of a bafflestone are the presence of a large number of in situ stalk-shaped fossils and a good imagination on the part of the geologist." (EMBRY & KLOVAN, 1971)

The data and interpretations presented above indicate that the Waulsortian mounds are bafflestone-boundstone biofacies (Fig. 1B) formed by mound-building guilds analogous to the frame-building guilds of Frasnian, Famennian and Viséan reefs (see below; Appendix 4).

Mound formation also required the copious production of lime mud, perhaps by abundant non-skeletal organisms (algae?; "different rules" taxa?) of unknown diversity and guild membership.

Thus, the Tournaisian mounds and biofacies resulted from ecologic-sedimentologic interactions among the producers of lime mud, the Baffler (sediment deposition) and Binder (sediment trapping, stabilization, retention) guilds. Previous research and the present guild-based analysis suggest that: 1) the ecological structure of mound-building guilds and frame-building guilds are analogous; the chief difference is the low volume of the Constructor Guild and high volume of the Baffler Guild in mound communities; 2) near end-member bafflestone biofacies (corner, Fig. 1A) are rare, largely confined to deeper waters of moderate turbulence and are most common in rocks of post-extinction ages; 3) near end-member bafflestones differ little from level-bottom biofacies in composition but differ significantly in the greater abundance of members of the Baffler and Binder Guilds; 4) application of the biologically mediated process of current baffling by suspension-feeding, erect growing members of the Baffler Guild provide useful insights for the interpretation of frameless biofacies ranging in size from thin-sections to mud mounds; 5) even if potential frame-builders (eg. calcareous algae, large solitary [*Amplexus*, Table 4] or small colonial corals) are present, they do not always build reefs; instead, deeper water mud mounds may

predominate over shallow water framework reefs; and 6) the Binder Guild is essential for trapping, stabilization and retention of sediment on mound summits, development of topographic relief and formation of dipping flank beds that characterize mud mounds; in framework reefs, relief and dipping flanks result from rates of upward growth of skeletal organisms that are more rapid than the rate of deposition on adjacent sedimentary substrates (FAGERSTROM, 1987).

The Waulsortian mud mound biota also suggests the need for upward revision of the water depths in the developmental history postulated by LEES et al. (1985) and LEES & MILLER (1985, in press). The various algae (filaments, stromatolites, cyanophytes, *Girvanella*; Appendix 4) probably lived in the photic zone (about 0-200+ m for Cyanophyta; about 0-150 m for codiacean chlorophytes). Furthermore, the large biomass of *in situ* fenestrate bryozoans and crinoids required moderate currents (5-10 cm/sec?; MCKINNEY et al., 1987) and abundant suspended organic matter to support life. At the depths postulated for Phases B-C (250-300+ m) by LEES & MILLER (1985, in press), the adequacy of such currents and concentrations of organics is uncertain (or doubtful?), especially during the switch from greenhouse to icehouse circulation, as occurred in the Late Devonian-Early Carboniferous (FISCHER, 1982, 1984), when circulation of deeper water was sluggish (WILDE & BERRY, 1984).

4 POST-TOURNAISIAN RECOVERY

The history of Early Carboniferous re-organization of framework reef communities is discussed by FAGERSTROM (1987, p. 371-378, 390-392). Of greatest importance in these communities, in both diversity and volume, are the algae, especially the four newly evolved groups with skeletons (i.e. phylloid, *Kamaena-Donzellia*, *Ungdarella-Stacheia*, *Tubiphytes*; CHUVASHOV & RIDING, 1984, Fig. 8; RIDING, 1977) and colonial Rugosa. *Girvanella*, stromatolites, Bryozoa and pelmatozoans generally maintained the same roles, but of lesser relative importance in these reef-building guilds, as they had in the Tournaisian mounds. Although framework reefs having this general composition have been described by several authors (eg. WOLFENDEN, 1958; ADAMS, 1983; WEBB, 1991), those of the Akiyoshi Limestone, southern Honshu Island, Japan are used here to exemplify a "typical" shallow water Visean community (see detailed descriptions in Ota [1968, 1977] and HAIKAWA & Ota [1978]).

The earliest Akiyoshi reefs are mid-late Visean (locally the *Nagatophyllum satoi* Zone) and dominated by large dendroid rugose corals (Constructor Guild), varied Bryozoa (Baffler-Binder Guilds), crinoids (Baffler) and stromatolites (Binder, Table 1; FAGERSTROM, 1987, p. 374-376, Pl. 42a). The chief factor distinguishing these frame-building guilds from those of the Famennian-Tournaisian is the emergence of newly evolved rugose corals with large, colonial coralla (Table 1).

The subsequent Carboniferous evolution in composition and guild structure of the Akiyoshi reef communities is documented by Ota (1968, p. 29-33, Pls. 2-13) and FAGERSTROM (1987, p. 375-378). It involves shifts in the relative

importance among members of the Constructor Guild, especially the Rugosa and Chaetetida (hypercalcified sponges) and stromatolites.

5 EVOLUTION OF REEF-BUILDING GUILDS AND BIOFACIES

In addition to the changes in taxonomic composition and diversity resulting from the Devonian extinction events and Early Carboniferous recovery discussed above, there were equally important changes in the reef-building guilds (Table 1). After assignment of individuals, colonies and taxa to particular guilds, the relative importance of these guilds in particular reef communities and biofacies can be measured and expressed by at least three different methods:

1. the relative taxonomic diversity in each guild (Fig. 1B). If diversity is low (eg. Tournaisian, Tab. 1), the guild membership of each taxon exerts strong influence on relative diversity.
2. the areal coverage (size) of each individual, colony and taxon in each guild and/or for the guild as a whole relative to other taxa and guilds. This method can be used for areal coverage data from horizontal surfaces, as in modern reefs, or from vertical surfaces, as in ancient reefs exposed in outcrops. The smaller the area studied, the less valid the measurements and the interpretations based on them, i.e. measurements from large outcrop surfaces are best (WEIDLICH, et al., 1993), those from large polished surfaces of ancient reefs are of intermediate value (NAGY, 1985) and those from hand specimens, cores and thin-sections are of doubtful importance for determining the overall guild structure of reef communities. Unfortunately, the latter have been used most commonly by paleoecologists and reef petrologists.
3. the relative volume of each taxon in each guild and/or for the guild as a whole (Fig. 1B). Such volumes are difficult to measure precisely but they can be estimated from closely spaced polished sections (ROWLAND, 1984).

For determining guild overlap (FAGERSTROM, 1987, 1988, 1991), the data from numbers 2 and 3 are the best quantitative methods. The data of Table 1 and the author's field observations are the basis for the interpretation presented in Fig. 1B. They clearly indicate an evolution in the paleoecological structure of these reef and mud mound examples as measured by the relative diversity and estimated volumetric importance of each reef-building guild and biofacies as follows:

1. Frasnian reef communities were characterized by relatively balanced taxonomic diversities in the reef-building guilds. However, estimated relative volumes of members of the reef-building guilds indicate that framestones predominate (Fig. 1B, points 1).
2. Famennian skeletal reefs were dominated by members of the Binder Guild producing typical boundstones (Fig. 1B, points 2, 3).
3. Tournaisian mud mounds, following the progressive extinction of the Frasnian-Famennian reef-building taxa of the Constructor Guild, are dominated by mound-building members of the Baffler and Binder Guilds producing mud-

rich, frameless bafflestone-boundstones (Fig. 1B, points 4).

4. The Visean initiated the gradual return of framework reefs and more evenly balanced reef-building guild structures (Fig. 1B, points 5). Although Visean reefs differ in composition and diversity from those of the Frasnian, they are similar in guild structure to Frasnian reefs (Fig. 1B, points 1).

This evolutionary sequence was driven by extinction-induced sequential changes in the composition and diversity of the reef-building guilds and changes in their relative importance. Compositional changes did not consist of post-extinction appearances of wholly new reef- and mound-building higher taxa or migration of taxa from level-bottom to reef communities; however, the major Tournaisian-Visean changes included appearances of new genera and species of colonial rugose corals. Although the extinction of all Devonian stromatoporoid and rugose coral species was complete by the end of the Famennian, a few genera and species of all other reef-building higher taxa survived each Devonian extinction. Furthermore, the capacity of extinction survivors to build reefs or mounds was diminished in the post-extinction guilds, with the exception of particular algae (eg. those of the Frasnian-Famennian). Thus, the Devonian extinction of reef communities differs from others by its longevity and its cumulative effects and from taxonomy-based mass extinctions in which high taxonomic turnover is concentrated at restricted stratigraphic horizons.

ACKNOWLEDGEMENTS

It is a pleasure to acknowledge, with appreciation, Alan Lees (Louvain) for discussions in correspondence and for reprints and a preprint on Waulsortian mounds that he so graciously provided, Eddy Poty (Liege) for sharing with me his most recent data on the distributions of Famennian-Tournaisian corals, Tomas Villamil (Boulder) for drafting Fig. 1 and Erik Flügel and Erentraud Flügel-Kahler for inviting me to publish my ideas in FACIES. The final manuscript benefitted greatly by thoughtful reviews of an early draft by Lees, who vigorously disagrees with my interpretation of the Waulsortian mounds, Erle Kauffman (Boulder) and Helmut Geldsetzer (Calgary)

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Manuscript received July 22, 1993

Revised manuscript received January 15, 1994

APPENDIX 1: GUILD ASSIGNMENTS OF DEVONIAN REEF-BUILDING ALGAL SPECIES, CANNING BASIN, NW AUSTRALIA (after WRAY, 1967, 1972; WRAY & PLAYFORD, 1970; PLAYFORD et al., 1976; RIDING & TOOMEY, 1972). All species occur in both the Frasnian and Famennian unless indicated.

<u>Species</u> *	<u>Guild Membership</u>	<u>Remarks</u>
<i>Renalcis devonicus</i>	Binder	encrusting
<i>R. turbitus</i>	Binder	encrusting
<i>Sphaerocodium</i> (= <i>Rothpletzella</i> ?)		
<i>magnum</i>	Baffler; Binder**	erect; encrusting
<i>S. exile</i>	Baffler; Binder**	erect; encrusting
stromatolites (mostly seaward slope)	Binder; Baffler**	encrusting; erect
<i>Paraepiphyton caritus</i>	Baffler; Binder**	erect; encrusting
<i>Girvanella wetheredi</i> (Frasnian only; mostly lagoonal)	Binder	encrusting
<i>Frutexites</i> sp. (a stromatolite?; mostly seaward slope)	Baffler; Binder**	erect; encrusting
<i>Solenopora</i> (or <i>Pseudosolenopora</i> ?)		
<i>geikiei</i>	Binder; Dweller	encrusting; rare
<i>Parachaetetes regularis</i>	Binder; Dweller	encrusting; rare
<i>G. irvanella ducii</i> (Famennian only; mostly lagoonal)	Binder; Dweller	encrusting; rare

* listed in approximate order of decreasing abundance. ** show evidence of morphological plasticity

APPENDIX 2: GUILD ASSIGNMENTS OF REEF-BUILDING STROMATOPOROID SPECIES

Species	Guild Membership; Guild Overlap	Remarks
SADLER AND PILLARA LIMESTONES, CANNING BASIN, NW AUSTRALIA (FRASNIAN) (after COCKBAIN, 1984; PLAYFORD & COCKBAIN, 1989)		
<i>Hermatostroma schlueteri</i>	Constructor; Binder*	subdominant
<i>H. roemeri</i>	Baffler	accessory
<i>H. ambiguuum</i>	Binder; Constructor	dominant
<i>H. perseptatum</i>	Binder; Constructor*	accessory
<i>Amhipora rudis</i>	Baffler; Constructor	dominant
<i>A. pervesiculata</i>	Baffler	accessory
<i>Actinostroma papillosum</i>	Constructor	subdominant
<i>A. papillosum</i> var. A	Constructor	accessory
<i>A. windjanicum</i>	Constructor	subdominant
<i>Clathrocoilona spissa</i>	Binder; Constructor	dominant
<i>Stachyodes costulata</i>	Baffler; Constructor	dominant
<i>S. australe</i>	Baffler	<i>in situ</i> ; accessory
<i>Stromatopora cooperi</i>	Binder; Constructor*	accessory
<i>S. minutitextum</i>	Constructor; Dweller	rare
<i>Stromatoporella laminata</i>	Binder	accessory
<i>Trupetostroma bassleri</i>	Constructor	accessory
<i>T. mclearnii</i>	Constructor; Baffler*	accessory
<i>Anostylostroma ponderosum</i>	Binder; Constructor*	accessory
WINDJANA LIMESTONE, CANNING BASIN, NW AUSTRALIA (FAMENNIAN) (after COCKBAIN, 1984; PLAYFORD & COCKBAIN, 1989)		
<i>Clathrocoilona saginata</i>	Binder	subdominant
<i>Stromatopora lennardensis</i>	Constructor	rare
WABAMUN FORMATION, ALBERTA, CANADA (FAMENNIAN) (after STEARN, 1988)		
<i>Labechia palliseri</i>	Constructor; Binder*	domal; laminar
<i>Stylostroma sinense</i>	Binder; Constructor*	laminar; domal
<i>Clathrostroma</i> cf. <i>jukkense</i>	Binder; Constructor*	tabular; domal
<i>Gerronostroma</i> sp.	Baffler	columnar,
	branching; rare	
<i>Stromatopora</i> sp.	Binder	tabular; rare

* show evidence of morphological plasticity

APPENDIX 3: GUILD ASSIGNMENTS OF DEVONIAN CORAL SPECIES, SADLER AND PILLARA LIMESTONES, CANNING BASIN, NW AUSTRALIA (after HILL & JELL, 1970; SORAUF & PEDDER, 1986)

Species	Guild membership; Remarks	Age
Solitary Rugosa		
<i>Catactotoechus irregularis</i>	Dweller; small coralla	Frasnian?; Famennian
<i>C. obliquus</i>	Dweller; small coralla	Frasnian
<i>Metriophyllum trochoides</i>	Dweller; small	Frasnian
<i>Syringaxon dickinsi</i>	Dweller; small	Frasnian; Famennian
<i>Temnophyllum turbinatum</i>	Dweller; small	Givetian?; Frasnian
<i>T. menyouseense</i>	Dweller; small	Givetian
<i>T. incomptum</i>	Dweller; small	Frasnian
<i>T. floriforme</i>	Dweller; small	Frasnian
<i>Zaphrentis iocosa</i>	Dweller; small	Frasnian; Famennian
Colonial Rugosa		
<i>Phacellophyllum</i> sp. B	Constructor	Frasnian
<i>Peneckiaella teichertii</i>	Constructor	Frasnian
<i>P.</i> sp. A	Constructor	Frasnian
<i>Haplothecia? lacinosia</i>	Dweller; rare, thamnasteroid	Frasnian
<i>Disphyllum caespitosum</i>	Constructor	Givetian; Frasnian
<i>D. virgatum</i>	Constructor	Frasnian
<i>D. curtum</i>	Constructor	Frasnian
<i>D.</i> sp. aff. <i>D. curtum</i>	Dweller; small coralla, may overlap Constructor Guild	Frasnian
<i>D. intertextum</i>	Constructor	Frasnian
<i>D.</i> sp. A	Constructor	Frasnian
<i>D.</i> sp. B	Constructor	Frasnian
<i>Hexagonaria playfordi</i>	Constructor	Frasnian
<i>Donia brevilamellata</i>	Constructor	Givetian; Frasnian
<i>Argutastrea hullensis</i>	Constructor	Givetian; Frasnian
Tabulata		
<i>Thamnopora angusta</i>	Constructor	Givetian?; Frasnian
<i>T. bolonensis</i>	Constructor	Frasnian
<i>Alveolites suborbicularis</i>	Binder; encrusting sheath	Givetian-Famennian
<i>A.</i> sp. cf. <i>saleei</i> *	Binder; lamellar, branching may overlap Constructor Guild	Frasnian
<i>A. tumidus</i> *	Baffler-Constructor; occurs as fragments or lamellae	Givetian; Frasnian
<i>A.</i> sp. cf. <i>intermixtus</i>	Binder	Late Devonian
<i>A.</i> sp. cf. <i>multiperforatus</i>	???	Late Devonian
<i>A.</i> sp. cf. <i>caudatus</i>	Baffler; slender branches	Givetian; Frasnian
<i>Aulopora</i> sp. cf. <i>liniformis</i>	Binder	Frasnian
<i>A.</i> sp. A	Binder; reptant, retiform net	Frasnian
* show evidence of morphological plasticity		

APPENDIX 4: GUILD MEMBERSHIP ASSIGNMENTS OF WAULSORTIAN (TOURNAISIAN) MOUND-BUILDING TAXA, DINANT BASIN, BELGIUM (Phases A-C of LEES & MILLER, 1985, in press; species diversity incomplete)

Taxon	Guild Membership; Remarks
Bryozoa	
<i>Fenestella</i>	Baffler; fenestrate
<i>Polypora</i>	Baffler; fenestrate
<i>Penniretopora</i>	Baffler; fenestrate
<i>Pseudonematopora</i>	Baffler; dendroid, branches unjointed
<i>Rhombopora</i>	Baffler; dendroid, branches jointed
anthrostylid indet.	Baffler; erect, dendroid?
* <i>Fistulipora</i>	Binder-Constructor; encrusting-massive
* <i>Leioclema</i>	uncertain
* <i>Stenopora</i>	uncertain
Other taxa	
Pelmatozoa (crinoids, especially Camerata; blastoids)	Baffler
hyalostelliids (siliceous sponges)	Baffler
filaments; cyanophytes (<i>Girvanella</i>)	Binder
<i>Amplexus</i> (Rugosa)	Constructor?/Dweller?; solitary, large, scolecoid; rare-common?
* show evidence of morphologic plasticity.	