Evaluating the Frasnian-Famennian mass extinction: Comparing brachiopod faunas

PAUL COPPER

The Frasnian-Famennian (F-F) mass extinctions saw the global loss of all genera belonging to the tropically confined order Atrypida (and Pentamerida): though Famennian forms have been reported in the literature, none can be confirmed. Losses were more severe during the Givetian (including the extinction of the suborder Davidsoniidina, and the reduction of the suborder Lissatrypidina to a single genus), but origination rates in the remaining suborder surviving into the Frasnian kept the group alive, though much reduced in biodiversity from the late Early and Middle Devonian. In the terminal phases of the late *Palmatolepis rhenana* and *P. linguiformis* zones at the end of the Frasnian, during which the last few Atrypidae declined, no new genera originated, and thus the Atrypida were extirpated. There is no evidence for an abrupt termination of all lineages at the F-F boundary, nor that the Atrypida were abundant at this time, since all groups were in decline and impoverished. Atrypida were well established in dysaerobic, muddy substrate, reef lagoonal and off-reef deeper water settings in the late Givetian and Frasnian, alongside a range of brachiopod orders which sailed through the F-F boundary: tropical shelf anoxia or hypoxia seems implausible as a cause for atrypid extinction. Glacial-interglacial climate cycles recorded in South America for the Late Devonian, and their synchronous global cooling effect in low latitudes, as well as loss of the reef habitat and shelf area reduction, remain as the most likely combined scenarios for the mass extinction events.

K e y   w o r d s : Brachiopoda, Atrypida, diversity, mass extinction, Kellwasser Crisis, Frasnian, Famennian, Devonian.

Paul Copper [pcopper@nickel.laurentian.ca], Department of Earth Sciences, Laurentian University, Sudbury, Canada P3E 2C6.

Introduction

The Frasnian-Famennian (F-F) boundary is defined by the lower boundary of the *Palmatolepis triangularis* (conodont) Zone, though rare occurrences of this species are in the *P. linguiformis* Zone beneath (Klapper *et al.* 1993). The designated type section is at the upper Coumiac quarry in the Montagne Noire in France, and the conodonts are cross referenced with goniatites, also representing nektoplanktic faunas in pelagic settings.

However, the brachiopod order Atrypida (like other shallower water benthic taxa) is not represented in strata near, or directly below, the F-F boundary either in the Montagne Noire, the Kellwasser Schmidt quarry in Germany, nor in the original Belgian type area of the Frasnian-Famennian boundary at Senzeilles. At Senzeilles, reef limestones with atrypids are overlain by nodular limestones, then the Matagne shales, the last of which have been correlated with the Upper Kellwasser Limestone (e.g., Dreesen *et al.* 1985; see also Godefroid & Helsen 1998). The general lack of atrypids and other brachiopods close to the F-F boundary almost worldwide has created previous problems in the sense that the tropical shelf faunas, and the deteriorating reef ecosystem, most strongly affected by the extinction, are usually not those most precisely dated with pelagic faunas. But many of these correlation problems have now been resolved with higher resolution data.

Global mass extinction episodes are biological phenomena identified by dramatic loss of biodiversity on a worldwide basis (Jablonski 1989; Erwin 1993; McGhee 1996); these bioevents cross sedimentary basins and oceans in low latitudes. Such very high extinction rates are normally marked by the order of 50% or more loss in biota at the genus level: decimation, i.e. a 10% loss, would not qualify as a mass extinction. Extinction events generally are also periods of very weak or zero origination rates, particularly during the nadir of biodiversity (the period prior to the common disappearance of lineages if the mass extinction is phased in, or the so-called dead zone following the extinction). If, or when, originations or replacements more or less match extinctions, biodiversity remains neutral, and no major decrease in total diversity is the result. Mass extinctions generally hit the marine biota of tropical and subtropical low latitudes hardest of all (Stanley 1987; Kauffman & Harries 1996), pointing to global climate and environmental change as prime, first order, culprits. However, the ultimate root(s) of the extinction itself, what caused climate or environmental change, may remain a puzzle. No global mass extinctions are known to have struck only, or primarily, the temperate to polar regions, but this is scarcely a novel revelation, since biodiversity decreases polewards in the high latitudes (except possibly for phytoplankton, in which diversity is related to nutrient supply, with the cold oceans richest in nitrogen and phosphorus). Mass extinction must thus be differentiated, and must be different in causality, from background extinction, that is, the normal ecological replacement of one taxon by another in the same niche. Another feature that characterises most global mass extinctions is the termination of high level lineages (to the level of orders or classes) which played a major role prior to the extinction event(s), e.g. the disappearance of (non-avian) dinosaurs in the late Cretaceous (these reptiles were never replaced by ecologically equivalent reptiles in the Cenozoic, but by mammals). Phyla, if these are biologically useful ranks, almost never disappear at mass extinction boundaries, though phylum losses are not unknown (if the Conodonta, dying off in the Triassic, or Graptolithina, in the Early Devonian, are accepted as phyla: curiously neither of these nektoplanktic index fossil groups vanished at any of the four dramatic global mass extinctions at the time).

For the F-F extinction, there was the disastrous loss of a number of tropical, benthic, shelly animals which never resurfaced in the Late Paleozoic, including the Atrypida and Pentamerida, two of the dominant shelly, benthic brachiopod orders of the Middle Paleozoic. Though the Frasnian was a period of relative cosmopolitanism featuring abundant (but lower diversity) brachiopod and reef faunas in tropical carbonate basins, it was not a period of major and rapid diversification and evolutionary innovation for

the atrypids: only seven new species-groups (subgenera or genera) arose in the Frasnian, with two of these possibly arising even in the preceding Givetian. Total diversity of the Atrypida for the Devonian was some 72 genera (Fig. 1), with only 15 genera/subgenera known from the Frasnian: the major decline was in the late Givetian with the loss of the atrypid suborder Davidsoniidina, and the all but total loss of the Lissatrypidina, with only a single genus, *Peratos*, from Germany (Copper & Gourvennec 1996). Thus the Frasnian continued a phase of decline for atrypid evolution that had commenced in the Givetian preceding. Long-lived lineages with records going back to the Middle Silurian (Wenlock), or even earlier, such as the Atrypinae, Spinatrypinae and Variatrypinae prevailed, with the Invertininae (including *Iowatrypa* and *Pseudogruenewaldtia*), arising in the Eifelian.

The compilation of papers in this volume attempts to document the F-F losses in the order Atrypida, a group of spire-bearing brachiopods typified by lophophores directed medially or dorsally, on a nearly global basis, and to update ranges and first-last appearances of taxa within the Late Devonian. The challenge of any faunal compendium covering a mass extinction interval is to demonstrate the nature and severity of the extinction event (and thus to provide a clue as to ultimate causality). This, of course, depends on at least two factors, (a) consistency in the taxonomy from one global region to another, and, (b) accuracy, as well as agreement, in the chronology of specific sections used as measures for the extinction event. This volume solves some of the taxonomic and correlation resolution problems for North America, Europe and China. The debate has also at times been sidetracked into opposing views by those who espouse the pelagic nektoplanktic faunas (e.g. ammonoids, conodonts) as providing the more accurate extinction scenario, versus those working with the neritic faunas derived from shelly and coralline organisms.
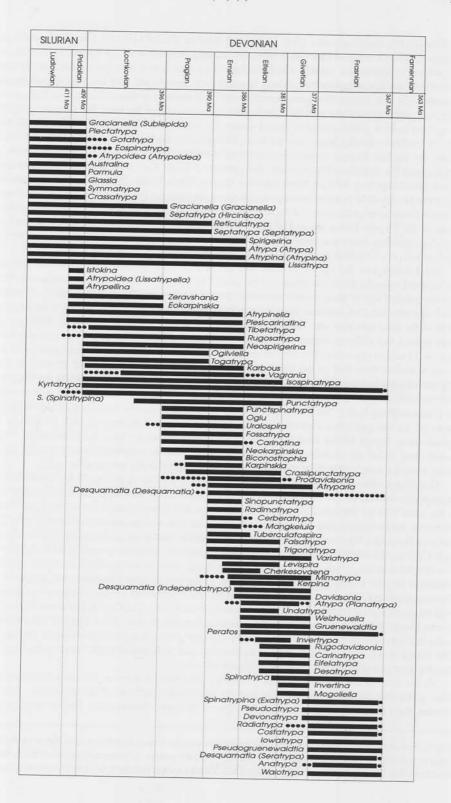
As Kauffman & Harries (1996) have pointed out, new and higher resolution faunal data at extinction boundaries challenge some of the more widely held shibboleths about global mass extinction events, i.e., (1) that mass extinctions were abrupt, (2) that mass extinctions were, or must be, non-selective because of their abruptness, and, (3) that recovery and radiation following mass extinction must be explosive. None of these truths appear to hold for the benthic faunas at the F-F mass extinction niveau. The F-F extinction, possibly the second greatest after the end Permian, provides fertile ground for research. This Late Devonian extinction looks increasingly more like a protracted series of taxon losses at a time of global ecosystem change (rise of first rain forests on land, dramatic oxygen increase, beginnings of Late Paleozoic glaciations, changeover to Pangea plate alignments, modification of surface and deep ocean currents). The F-F extinction selectively kicked out the mid-Paleozoic tropical carbonate shelf biota, especially in the reef and peri-reefal setting, wiping out the keystone stromatoporoids, corals and shelly benthos, but retaining the stress-resistant calcimicrobes that sailed through the event, and which even marked a post-extinction abundance boom. And, the post-extinction Famennian recovery phase looks increasingly less like a phase of explosive radiation, but more like a gradual, protracted, but very limited long term recovery of 4–5 Ma, featuring expansion of climatically more tolerant/resistant orders for the brachiopods (e.g., stocks like spiriferids, athyrids, rhynchonellids, and terebratulids, which survived even the end Permian, and end Triassic mass extinctions later), and an extended absence or sparsity of invertebrate built reefs. Famennian environments were repopulated progressively by taxa with Carboniferous affinities: one could even argue that the Carbonife-

rous should have stratigraphically begun with the Famennian, one stage earlier (indeed many Famennian strata have been assigned in the past to the Carboniferous).

Nearly every mass extinction event appears to create its own new dogma in the literature, the F-F being no exception. Some of these dogmas are cyclical, depending on what new data is published at the time, and how that may support one theory or another. The dogmas usually have a long record in the literature, reflecting the evidence as seen from one continent or another, or the previously established bias against it. Some of the following assumptions or concepts have been very current in the last twenty years: (a) the Famennian was typified by large scale transgressions, there were no major regressions in the Famennian, and the F-F boundary was entirely transgressive; (b) the Famennian was dominated by global greenhouse climates similar to those of the Middle Devonian (above average warming), and there was no marked glaciation in South America (or elsewhere) until the Late Carboniferous; (c) Famennian black shales can only represent deepening and transgressive, anoxic episodes in a stagnant, sluggish ocean, and therefore provide a clear signature of global warming and flooding of shallow tropical shelves; (d) the Malvinokaffric (Emsian–Givetian) fauna cannot be used as an example of Late Devonian cold climates and cold water faunas, because it was not Frasnian in age; and, (e) there was a large East-West ocean between Gondwana and Laurussia in the Late Devonian, and no cold currents were possible in low latitudes. Some of these beliefs can now be safely set aside, or modified, with the new evidence.

Atrypid gains and losses in the Devonian

The Devonian marked the greatest period of diversification in the order Atrypida, with ca. 72 genera and subgenera ranging partly or wholly through the period (Fig. 1), and the presence of three of four atrypid suborders, the Atrypidina, Lissatrypidina and Davidsoniidina (the Anazygidina, a primarily Ordovician suborder, are last known from the Wenlock–Ludlow). The precise first and last appearances of these taxa are uncertain, since these depend on which species are included or excluded (i.e. how broad the taxon is perceived), and the correlation precision of strata that house the oldest and youngest species. Thus the data are in need of refinement, with ranges extended to the end of substages if they were not accurately known: within stage diversity increases or declines at the genus level are not apparent, as they were in other compilations (Copper 1986). In terms of total biodiversity, the Emsian defined the acme with some 41 species-groups. The Frasnian ranks as the period of lowest diversity during the Devonian, with about 15 genus level taxa, probably largely because of the end of the davidsoniids. Within the Frasnian itself, overall brachiopod species and genus losses show a maximum of diversity in the early Frasnian with progressive losses, and lower origination rates, towards the F-F boundary, and maximal turnover within the final *P. linguiformis* Zone (Baliński 1996; Godefroid & Helsen 1998; Racki 1998; Racki & Baliński 1998). This suggests that the extinctions were spread over ca. 10 million years, the duration of the Frasnian, and that there was no peak in diversity at the end of the Frasnian, followed by catastrophic instantaneous loss. If conodont stages last on average ca. 500,000 years, the turnover within the final *P. linguiformis* Zone itself could mark a protracted period of severe disturbance.

→

Fig. 1. Extinction range chart of the genera/subgenera of the order Atrypida, grouping extinction episodes through the Devonian (data to mid-1997). No abundance figures are shown, and taxa are not grouped by families or subfamilies. All ranges are generally extended to the end of stages, unless fresh data dictate otherwise; thus the end of the Frasnian is shown as relatively abrupt for lineages, which is certainly not so on a regional, or even global basis (see Racki 1998).

Stratigraphic range chart of atrypid brachiopod genera across the Silurian and Devonian. Time scale columns: SILURIAN (Ludlowian, Pridolian) and DEVONIAN (Lochkovian, Pragian, Emsian, Eifelian, Givetian, Frasnian, Famennian), with age markers 411 Ma, 409 Ma, 396 Ma, 390 Ma, 386 Ma, 381 Ma, 377 Ma, 367 Ma, 363 Ma.

Taxa shown (top to bottom):
Gracianella (Sublepida), Plectatrypa, Gotatrypa, Eospinatrypa, Atrypoidea (Atrypoidea), Australina, Parmula, Glassia, Symmatrypa, Crassatrypa, Gracianella (Gracianella), Septatrypa (Hircinisca), Reticulatrypa, Septatrypa (Septatrypa), Spirigerina, Atrypa (Atrypa), Atrypina (Atrypina), Lissatrypa, Istokina, Atrypoidea (Lissatrypella), Atrypellina, Zeravshania, Eokarpinskia, Atrypinella, Plesicarinatina, Tibetatrypa, Rugosatrypa, Neospirigerina, Ogilviella, Togatrypa, Karbous, Vagrania, Isospinatrypa, Kyrtatrypa, S. (Spinatrypina), Punctatrypa, Punctspinatrypa, Oglu, Uralospira, Fossatrypa, Carinatina, Neokarpinskia, Biconostrophia, Karpinskia, Crassipunctatrypa, Prodavidsonia, Atryparia, Desquamatia (Desquamatia), Sinopunctatrypa, Radimatrypa, Cerberatrypa, Mangkeluia, Tuberculatospira, Falsatrypa, Trigonatrypa, Variatrypa, Levispira, Cherkesovaena, Mimatrypa, Kerpina, Desquamatia (Independatrypa), Davidsonia, Atrypa (Planatrypa), Undatrypa, Weizhouella, Gruenewaldtia, Peratos, Invertrypa, Rugodavidsonia, Carinatrypa, Eifelatrypa, Desatrypa, Spinatrypa, Invertina, Mogoliella, Spinatrypina (Exatrypa), Pseudoatrypa, Devonatrypa, Radiatrypa, Costatrypa, Iowatrypa, Pseudogruenewaldtia, Desquamatia (Seratrypa), Anatrypa, Waiotrypa.
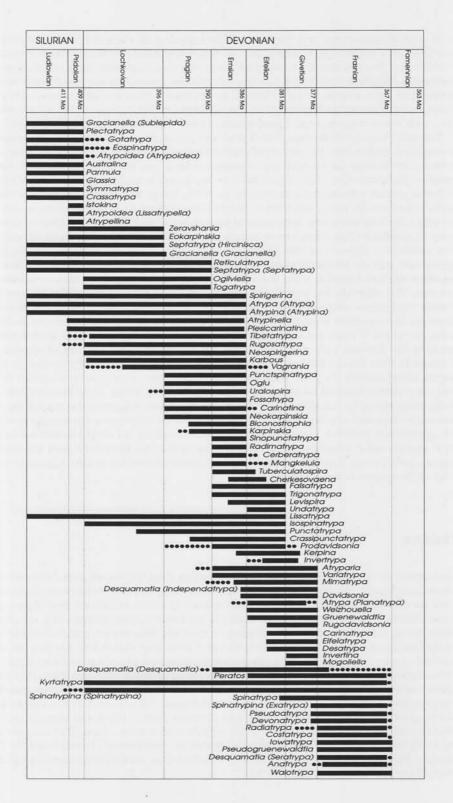
Measured in extinction rates (Fig. 1), the end Silurian (Pridoli) saw the loss of 14 genera and subgenera, though some of these have been sporadically reported from the earliest Devonian, e.g. *Atrypoidea*, or depend on variable identifications of such taxa as *Gotatrypa* (which may be early *Kyrtatrypa*), and *Eospinatrypa* (which may be small early *Spinatrypa*). The Lochkovian and Pragian each saw only four genera disappear, possibly merely an example of faunal turnover or background extinction, and some of these may have been gone before the end of this time. The Emsian, generally recognized to be a global period of faunal marine provincialism, with many unique endemic taxa (e.g., in the Urals, South China), saw the loss of 22 taxa, similar to the combined Middle Devonian losses. By the late Emsian, cosmopolitan faunas were the rule, with an Old World province, an Appalachian (or Appohimchi) province, and possibly a South East Asia province, but with some faunal interchange (e.g. western North America, Europe, Urals, South China). This cosmopolitanism may have provided the competition required to eliminate endemic forms, or may have enabled some endemic forms to migrate more widely to wipe out more abundant and previously widespread taxa. Some of the 22 taxa lost at the end of the Early Devonian, may also have continued beyond this boundary, pending taxon reassessment, e.g. did *Carinatina* persist into the Eifelian or evolve into *Eifelatrypa*?; did *Vagrania* grade into *Desatrypa* in the Eifelian?

The Eifelian saw the last of 11 taxa, and the end Givetian marked the end of the primarily reef-adapted suborder Davidsoniidina, and the loss of 14 taxa. Thus, the Middle Devonian combined saw the greatest loss of taxa, slightly exceeding that of the Emsian. The complete range of Frasnian taxa is not yet clear. *Desquamatia (Desquamatia)* appears to have gone before the end of the stage, but some of the other taxa may also have disappeared within this time, and not at the end. Different taxa seem to have had different ranges on various continents, thus regional diversity was probably lower than 14–15 taxa in any one setting. By the end of Frasnian time, the 14 dominant taxa were gone: total losses were less than that of the Emsian and Givetian. This in itself is not so remarkable since origination rates and overall diversity were lower in the Frasnian than at any time in the Devonian. Only one smooth genus, *Peratos*, known only from a single reefal species in Germany, was present in the Frasnian (Iberg Kalk), thus diversity is virtually entirely measured by one suborder, the Atrypidina. Some of the last persistent survivors appear to have been the long-ranging taxa *Spinatrypa* and *Spinatrypina*, though locally *Iowatrypa* may be among the last survivors in the *Palmatolepis linguiformis* Zone. None are definitively known from the Famennian anywhere; though isolated reports occur, these are now known to be reworked faunas or stratigraphically misidentified units.

Origination rates of atrypid taxa can also be evaluated for the Devonian (Fig. 2). Devonian Atrypida originating below the Siluro–Devonian boundary comprise 12 taxa, with the possibility of another three in the latest Silurian (Pridoli: *Tibetatrypa, Rugosatrypa* and *Spinatrypina*). One of the Late Silurian suborders, the Davidsoniidina, arose in the Ludlovian, but came to dominate the reef setting in the Early and Mid-Devonian. Nine atrypid genera appear at or near the base of the Lochkovian, with *Punctatrypa* added late in the Lochkov, probably derived from *Atrypinella* (which has its roots in the Late Silurian). The Pragian saw the arrival of nine genera or subgenera, some appearing later than others, and three additional Emsian genera possibly also appearing in the late Pragian (*Desquamatia, Atryparia* and *Crassipunctatrypa*). Therefore both the Lochkovian and Pragian saw an overall increase in diversity with origination gains exceeding extinction losses by at least 50%. The Emsian saw some 17 new taxa evolve (some of these possibly prior to this, and some towards the end of the Emsian). This marks an acme in origination within the Devonian, a very vigorous period of expansion leading to the classical Old World Mid-Devonian fauna, highest in diversity, and with probably the most widespread reef development and globally warmest mid-Paleozoic climates.

At the base of the Eifelian (Middle Devonian), five new taxa arose, with five others arriving later within the Eifelian, mostly in the mid- to late Eifelian episode of diversification: after the Emsian, the Eifelian saw the second largest increase in atrypid biodiversity. The Givetian marks a

→

Fig. 2. First occurrence range chart grouping originations of the genera or subgenera of the order Atrypida (data to mid-1997). This demonstrates low Frasnian origination rates, and zero origination towards the F-F boundary. The Emsian–Eifelian marks maximal originations for the Atrypida, with the Frasnian the lowest.

Stratigraphic range chart of atrypide brachiopod genera across the Silurian (Ludlowian, Pridolian) and Devonian (Lochkovian, Pragian, Emsian, Eifelian, Givetian, Frasnian, Famennian) stages, with age markers at 411 Ma, 409 Ma, 396 Ma, 390 Ma, 386 Ma, 381 Ma, 377 Ma, 367 Ma, and 363 Ma.

Taxa listed:
Gracianella (Sublepida)
Plectatrypa
Gotatrypa
Eospinatrypa
Atrypoidea (Atrypoidea)
Australina
Parmula
Glassia
Symmatrypa
Crassatrypa
Istokina
Atrypoidea (Lissatrypella)
Atrypellina
Zeravshania
Eokarpinskia
Septatrypa (Hircinisca)
Gracianella (Gracianella)
Reticulatrypa
Septatrypa (Septatrypa)
Ogilviella
Togatrypa
Spirigerina
Atrypa (Atrypa)
Atrypina (Atrypina)
Atrypinella
Plesiocarinatina
Tibetatrypa
Rugosatrypa
Neospirigerina
Karbous
Vagrania
Punctspinatrypa
Oglu
Uralospira
Fossatrypa
Carinatina
Neokarpinskia
Biconostrophia
Karpinskia
Sinopunctatrypa
Radimatrypa
Cerberatrypa
Mangkeluia
Tuberculatospira
Cherkesovaena
Falsatrypa
Trigonatrypa
Levispira
Undatrypa
Lissatrypa
Isospinatrypa
Punctatrypa
Crassipunctatrypa
Prodavidsonia
Kerpina
Invertrypa
Atryparia
Variatrypa
Mimatrypa
Desquamatia (Independatrypa)
Davidsonia
Atrypa (Planatrypa)
Weizhouella
Gruenewaldtia
Rugodavidsonia
Carinatrypa
Eifelatrypa
Desatrypa
Invertina
Mogoliella
Desquamatia (Desquamatia)
Peratos
Kyrtatrypa
Spinatrypina (Spinatrypina)
Spinatrypa
Spinatrypina (Exatrypa)
Pseudoatrypa
Devonatrypa
Radiatrypa
Costatrypa
Iowatrypa
Pseudogruenewaldtia
Desquamatia (Seratrypa)
Anatrypa
Waiotrypa

low episode of origination of only two taxa near the beginning and the spread of three others late in the Givetian, *Pseudoatrypa, Exatrypa*, and *Devonatrypa*, taxa that played a significant role early in the Frasnian. *Invertina* may have arrived later in the Givetian, rather than earlier, and the Central Asian genus *Mogoliella*, may be a senior synonym of *Carinatrypa*, thus it is possible that only a single atrypid genus arose in the early Givetian, though many Eifelian taxa were retained. The end of the Givetian also marks a high extinction rate of 14 taxa (see Fig. 1), marking this as an unusual period with lowest origination and highest extinction rates within the Devonian Atrypida.

The early Frasnian saw the expansion of seven new genera, but some had arrived already in the Givetian (e.g., *Radiatrypa*). The only significant new genera to appear at this time belonged to the distinctive Invertininae, i.e. the relatively cosmopolitan *Iowatrypa*, and the NE European–N Urals genus*Pseudogruenewaldtia*. Some regard the latter two genera as forming a distinctive subfamily, the Pseudogruenewaldtiinae (Rzhonsnitskaya *et al.* 1997), though their internal structures are very similar to the *Invertina* group, which has its origins in the Eifelian. As a result, the Frasnian had at best only a low origination rate, comparable to the low rate of the Givetian, all within the ribbed, conservative suborder Atrypidina, a group with origins in the Middle Ordovician, nearly 100 million years earlier. The Atrypida became extinct at, or near the end of, the Frasnian, and no new supraspecific taxa are known to appear in the late Frasnian: there was no arrival of potential progenitor taxa with a possibly wider adaptive, climatically tolerant range to repopulate the Famennian seas. This relatively low overall Frasnian diversity is accentuated regionally: in Iowa for example, the Frasnian sees only six taxa, *Spinatrypa, Spinatrypina, Pseudoatrypa, Devonatrypa, Costatrypa* and *Iowatrypa*, which is probably high to average for any shelf area at the time. In some basins, diversity at this time was reduced to one or two genera or subgenera. One of the interesting aspects is that Frasnian reefs generally contain few atrypid taxa, and low atrypid abundance, compared to their Emsian–Eifelian counterparts, and none appear specifically adapted to reef settings, except possibly the pedicle-fixed subgenus *Spinatrypina (Exatrypa)*, which occurs commonly in perireefal crinoidal thickets, or the Rasenriff, backreef setting. If the Frasnian were an ideally warm setting for encouraging reef expansion, as has been suggested, the atrypids did not show any evolutionary or ecological response. At best the order's reaction was to remain conservative, stagnant and generalist. Large size also was not favoured: the last atrypid species within the late *P. rhenana* and *P. linguiformis* zones tended to be smaller than those in the early and middle Frasnian, and Givetian. Thus strong extinction pulses, combined with low to zero origination rates, killed off the atrypids in the late Frasnian.

Causes

The existence of five major Phanerozoic mass extinctions (Late Ordovician, Late Devonian, end Permian, end Triassic, and end Cretaceous) is, these days, rarely disputed, though some might wish to add the ongoing Pleistocene extinctions, and late Early Cambrian extinctions. Nevertheless, the interpretations of causes, and the relative scaling of the events (timing, severity, etc), still create acerbic debate, and are a major bone of contention for those who fall into one causal camp or another. For the Late Devonian extinction this also holds true. Causes must explain how and why the Late Devonian crises were long term events, either gradual or stepdown, played out over several million years and affecting many groups from the end Givetian through Frasnian (McGhee 1996). They must explain correlations between eustatic events and extinctions, and how evolutionary change preceded or accompanied the extinctions (Feist 1991; Johnson & Klapper 1992; Oliver & Pedder 1994). They must be able to interpret connections between Late Devonian glacial – interglacial intervals, and the selective nature of the F-F event in affecting primarily the tropical marine biota. They must explain why nearly invariably the coral-stromatoporoid reefs died out meters to tens of meters below the F-F boundary. They must explain why eurythermal cool shallow water and cool deep water invertebrates preferentially survived the extinctions.

Cooling climates. — That the Late Devonian mass extinction was caused by cooling/glaciation was first suggested by Copper (1975, 1977) on the basis of the Famennian survival of cold and deep water orders of brachiopods, versus the loss of tropical orders and reef biota. This was corroborated by the subsequent description of Late Devonian glacial features and glaciomarine sediments from South America (Caputo 1985; Caputo & Crowell 1985; Martinez & Isaacson 1996; Isaacson 1997). Late Devonian cooling and glaciation was disputed by Thompson & Newton (1989) and Brand (1989), on the basis of $\delta^{13}C$ and $\delta^{18}O$ stable isotope signatures, but other stable isotope data conflict with this (Wang *et al.* 1991). However, dramatic sealevel drawdown at the F-F boundary, and repeatedly for the Famennian, is no longer in question (Johnson & Klapper 1992). A major regression is accepted either towards the top of the UKW or at the base of the Famennian (Casier & Devleeschouwer 1995), or both. An oxygenation event (3.5 m below the overlying Famennian Senzeilles Shale) occurs in the dysaerobic Matagne shales, with dwarfed, low diversity brachiopod faunas commonly correlated with the UKW (Casier 1992): this probably indicates watermass overturning just below the F-F contact.

The single most dramatic drop in RCO_2 for the whole of the Phanerozoic is now well documented for the Late Devonian interval at 380–350 Ma (Berner 1994, 1997). Wilder (1989) and Algeo *et al.* (1994) suggested that this was due to the arrival of the first tropical rain forests (pumping O_2 into the atmosphere, storing C as coal), and concomitant changes in weathering profiles. Retallack (1997) proposed that early forest soils may have been a prime agent in accelerating silicate weathering (absorbing CO_2, and releasing O_2), a process that may even have started in the Givetian (*Schmidtognathus herrmani–Polygnathus cristatus* and *P. varcus* zones), well before the appearance of coals and large trunks, thus speeding up the decline of the mid-Paleozoic greenhouse. Whatever the ultimate cause, a dramatic rise in seasurface phytoplankton (leading to organic rich shales: Pedersen & Calvert 1990), the rise of rainforests, or accelerated silicate weathering, O_2 increase and CO_2 decline mark the icehouse effect. The lowering of CO_2 values accentuates cooling temperatures, shrinking tropical latitudes, and reduced river runoff, and promotes drier climates (which have a balancing effect on soil weathering).

Probably the single most severe control on reef growth is cold water: maximal coral diversity and reef distribution today centres around equatorial latitudes, and decreases dramatically polewards (Veron 1995). Tropical carbonate reef growth is not sustained in higher latitudes because carbonate secretion slows down, and zooxanthellate reef organisms are metabolically confined to tropical waters, in the same sense that the tropical rainforest is limited by temperature and moisture (Hubbell 1997). Cooling of the low tropical latitudes, because of high latitude glaciation, and/or shifts in distribution of cold, deep waters, produces a cascade of effects inimical to the reef ecosystem: (a) it slows down $CaCO_3$ precipitation as temperatures fall, (b) kills of the stenothermal tropical taxa, (c) brings up cool deep waters with nutrients, which in turn inhibit $CaCO_3$ precipitation, and (d) lowers sealevel and reduces shelf area available, and/or eliminates the shallowest biotas of the reef flat, back reef and shallow forereef (increasing competition for remaining niche space). The conventional view of high latitude cooling in the past was that it largely spared the tropics, except possibly shrinking the tropical boundaries (thus saving reefs and rainforests): however, this concept has had to be abandoned with data showing that tropical sea temperatures also dropped by as much as 5°C during the Pleistocene ice ages (Guilderson *et al.* 1994; Beck *et al.* 1997; Webb *et al.* 1997), and that the reef belt and tropical land areas were not insulated from polar cooling.

The Devonian brachiopods of South America, assigned by Boucot *et al.* (1969) to a cold water, Gondwanan Malvinokaffric realm are instructive in terms of their content, and environmental setting. Their cold climate affinities are undisputed; carbonates and reefs are absent. The Devonian Parana Basin faunas of Brazil, Uruguay, and related basins of the Malvinas and South Africa (Clarke 1913; Copper 1977) are dominated by the rhynchonellid *Australocoelia*, large spiriferids such as *Australospirifer*, the large inarticulate *Orbiculoidea*, and bivalves: these brachiopods numerically form more than 70% of the fauna, with terebratulids more common in the Mato Grosso area. All these Emsian–Givetian taxa belong to eurythermal orders which survived the F-F extinction in the low latitudes. Rhynchonellids and terebratulids today occupy only high latitude cool water shelves, or occur in deep waters (H < 1500 m) of the tropics. The common Spiriferida, and lesser Athyrida, common cool water

inhabitants of the Late Paleozoic of Gondwana, lasted through the Early Jurassic, surviving two more global mass extinction events. The tropical Atrypida and Pentamerida are completely absent in the Mavinokaffric realm, being unknown from South America (except in northern Venezuela), the Malvinas islands, Antarctica, and South Africa. A similar feature is seen in the remaining neigbouring basins of Bolivia, Peru and Chile (Isaacson & Saablock 1989; Isaacson 1993), where the order Terebratulida makes up more than 40% of the faunas, and a more diverse brachiopod fauna is evident, including the order Athyrida [note, however, that Isaacsaon (1993) attributed the leptocoeliid brachiopods like *Australocoelia* to the order Atrypida, and conversely assigned the schuchertellids to the atrypid superfamily Davidsonioidea]. By the end of the Givetian the Malvinokaffric brachiopod fauna was gone: these areas show no brachiopods surviving, therefore marking extremely inhospitable surroundings for normal marine shelly benthic taxa. These strata yield only miospores, and mixed fresh, brackish and marine cool water invertebrate assemblages: by the Frasnian, much of the South American basins was above sealevel, shorelines had retreated, and the remaining faunas were impoverished, or strata provide no megafossils (Copper 1977; Barrett & Isaacson 1989).

Warming. — Prior to 1974, only globally warm, hothouse climates were thought to be possible for the Late Devonian, and the Frasnian and Famennian were lumped both in terms of postulated large scale transgressions-flooding of continent interiors and Devonian warm climates. McLaren (1970) excluded both Famennian cooling/glaciation, as well as warming, as possible mechanisms for extinctions. This changed somewhat after the discovery of Late Devonian glaciation events by Caputo & Crowell (1985), though the dating of these South American tillites/diamictites, dropstones, striae, etc. was disputed as being Carboniferous. Cool thinking reverted to the hot hypothesis when Sheridan (1987), on the basis of tectonics, and Brand (1989: p. 312), using stable isotope brachiopod results from three samples at or near the F-F boundary (localities labelled Geneseo, Grenzschiefer, Famenne Schiefer), stated that the Frasnian through Famennian oceans developed mean temperatures above 38°C (at the F-F peak), well beyond threshold levels at which coral reefs and benthic life could be sustained, and/or that oceans had salinities of < 20 ppt (the latter can be excluded as implausible). Brand stated that these were the causes of the F-F crises, though the very limited sample size, and lack of data available as to which levels were sampled, is not convincing. Such abnormally high sea surface temperatures and salinities are clearly unrealistic, even during possible interglacial Late Devonian oscillations. Thompson & Newton (1989) proposed episodic warming as the killing factor in the F-F extinction, citing examples of heat intolerance in modern organisms, amplification of the oxygen minimum levels as being caused by warming (black shales), and a single catastrophic event at the end of the Frasnian. However, it is exactly the tropical taxa that are most affected, with repopulation of the Famennian seas by cool tolerant and deeper-cooler water brachiopods (rhynchonellids, terebratulids), and the Late Paleozoic cool water, high latitude Gondwana orders, the spiriferids, athyrids, and productids that survived the Famennian and which were so dominant in the cold water regimes of the Devonian (Copper 1977). Sorauf & Pedder (1986) noted that the corals which survived the F-F events were the deeper, colder water solitary forms. Stearn (1987) suggested that the repopulation of the Famennian stromatoporoid biota by the labechiids (which had survived the glacial Late Ordovician extinction), was due to cold water tolerance. McGhee (1982, 1996) remarked on the explosive expansion of the glass and lithistid sponges in New York, W Canada, Poland, and Australia: such sponges normally occupied a Paleozoic deeper, cool water, off-shelf habitat. These clues do not support warming as a cause, though Thompson & Newton (1989) dismissed these as shallow niche takeover once the shelf was depopulated. Baliński (1996) identified a dwarfed, deeper water brachiopod fauna in the Polish late Frasnian (though this could be variably interpreted), and a distinct regressive pulse below the F-F boundary. This dwarfing matches ostracode observations in Belgium and France (Casier 1992; Lethiers & Casier 1994). Lethiers & Casier (1992) suggested that the surviving and recovering Famennian ostracodes were derived from groups which lived in sheltered, oxygenated nearshore environments, and that there is no evidence for anoxia accounting for the disappearance of 70% of the ostracodes (Casiers & Lethier 1997). To date no tropical, oxygenated shelf refugia, which might have housed a recovery brachiopod fauna, are known from the F-F boundary.

Buggisch (1991) played on a variation of the warming theme by suggesting that warm climates stimulated plankton productivity, which then led to high CO_2 losses with burial, and increased O_2 levels due to photosynthesis, which in turn was postulated to lead to autocyclic cooling. Becker & House (1994), basing their data on nektoplanktic ammonoids, favoured greenhouse overheating, in tandem with sealevel oscillations and hypoxia (from rapid flooding and transgression), as the causes for the F-F extinctions. However, both views contradict modern observed distribution patterns of plankton productivity and climate: plankton productivity is accelerated in high latitudes, where cool, deep water brings up nutrients (diatoms are most diverse and abundant in the south polar seas today). Radiolarian diversity and abundance is highest in tropical latitudes on the west sides of continents, W Africa, W Australia and Indonesia, W coast Americas, because of N and P nutrient upwelling (the phytoplankton supplying the radiolarians). Cold, deep waters are capable of storing larger amounts of CO_2: the retention and expansion of CO_2 in the oceans during global cooling, would decrease the amount circulating into the atmosphere, and have a positive feedback in maintaining higher levels of atmospheric icehouse oxygen (Franois *et al.* 1997). The CCD rises as temperatures fall. The Polish *P. linguiformis* Zone (just below the F-F boundary) is instructive here (see Racki & Baliński 1998): it features radiolarians and glass sponges, which correlate with cold upwelling in low latitudes.

Though it is possible that elevated sea temperatures can trigger partial coral bleaching locally, as suggested in relation to ENSOs (El Niño Southern Oscillations: Glynn & D'Croz 1990; Glynn 1993), these are extremely short-lived decadal cycles, and are not known to be permanent, nor worldwide. Bleaching has also been related to high solar irradiance, and disease, and suggested to be an adaptive mechanism for switching symbionts (Buddemeier & Fautin 1993). Formerly bleached areas of the Caribbean and the Java Sea have recovered, similar to the recovery from *Acanthaster* invasions in the Indo-Pacific, and other areas have been rebleached without total reef collapse (Brown 1997). In other areas (e.g., Gulf of Phuket,Thailand), elevated sea temperatures have produced little reef mortality, and have been more severe on the outer than inner reef, though bleaching took place; anthropogenic damage is far more stressful (Brown 1997). Elevated sea temperatures appear to be more critical in the cool eastern Pacific, where mean sea surface temperatures are much lower, reefs are scarce, and coral diversity is down to less than 10 species (Glynn 1993). The Sulu Sea, straddling the area between the Philippines and Indonesia, has the highest mean annual SSTs (seasurface temperatures) anywhere on earth today (Linsley 1996); it is the same area that intersects the highest coral biodiversity today, more than 800 coral species, versus ca. 500 for the Great barrier Reef (Veron 1995), whose southern margin is in the temperate zone. Thus higher SSTs correlate with coral diversity and reef growth: it seems highly unlikely that such a situation was reversed in the Late Devonian, as those who equate reef extinction with warming suggest.

The very few stable isotope signatures determined for the F-F interval are still controversial. The three specimens sampled by Brand (1989) around the F-F boundary are not tied in to conodont zones and could cover intervals of several million years: none came from the *P. linguiformis* Zone. Previous samples are equally sparse and inconclusive (Popp *et al.* 1986), contrary to much effort cited by Thompson & Newton (1988). Wang *et al.* (1991) and Yan *et al.* (1993) recorded a double negative $\delta^{13}C$ (loss of surface productivity) and positive $\delta^{18}O$ excursions (cooling signatures) just below the F-F and at the F-F boundary in China, the contrary to warming signatures claimed by others. Baliński (1996) plotted a rise in $\delta^{13}C$ and fall in $\delta^{18}O$ (warming) in the latest Frasnian just below the F-F boundary, and the reverse in the lowest Famennian *P. triangularis* Zone, but the differences were less than 2‰, and not significant. This evidence is thus ambiguous. The Famennian was clearly not a protracted 4 million year long glacial interval, and thus some samples should show interglacial warming and others cooling. This is reflected in the cooling shown for samples from the Famennian Griotte (Unit 84: Brand & Legrand-Blain 1992). What are lacking are consistently sampled brachiopods throughout the Frasnian and Famennian. New evidence (Martinez & Isaacson 1996; Isaacson 1997) demonstrates that glaciation occurred over a very broad area of Brazil and Bolivia, including dropstones accurately dated by palynozones, and that South American Late Devonian glaciation is reflected in the numerous regressive cycles featured in continental basins of North America, and elsewhere, particularly in the Famennian (Grader & Isaacson 1997; Veevers &

Powell 1987). It is difficult to reconcile the strong evidence for Famennian glaciation with the super warm Late Devonian ocean data presented by others. There is also little firm evidence to indicate that tropical organisms are much more affected by warming than cooling, as stated by Thompson & Newton (1988). To the contrary, during warming episodes organisms can migrate to higher latitudes (as shown abundantly throughout the hothouse mid-Paleozoic), an option not available during cooling, when the tropics shrank, with the tropics themselves known to have cooled dramatically by 4–8°C during Pleistocene glacial intervals (Guilderson *et al.* 1994; Beck *et al.* 1997).

The warming hypothesis suffers from major problems: (1) warming correlates poorly with regressive cycles typical of the Famennian, and in the late Frasnian *P. linguiformis* Zone, terminating in a regressive event. If glacial cycles mark the end Frasnian-beginning Famennian regression (Caputo 1985; Veevers & Powell 1987; Isaacson 1997), and regression at the Givetian terminus, then warming should accompany transgression, the opposite of that observed at the F-F boundary; (2) seasurface warming might stimulate terrestrial, coastal lowland plant growth, but would act as a depressant on phytoplankton productivity as warm waters are poorer in nutrients than cold, and warm waters would block the upwelling of nutrient rich, cold bottom waters (the ENSO effect), necessary to stimulate phytoplankton photosynthesis; (3) carbonate platform tropical benthos were the most catastrophically affected F-F ecosystems. Warming would, in contrast, expand the areas capable of sustaining reef growth, especially into higher latitudes (e.g. as seen in the Bermuda reefs with the establishment of the warm Gulf Stream). The largest reef systems ever known, during the Siluro–Devonian (and Phanerozoic), occurred when global seasurface temperatures averaged 5–10°C higher than today's. The most reduced Phanerozoic reef ecosystems were during the icehouse Carboniferous–Permian, when coral reefs effectively disappeared, and only mudmounds existed. This was probably even worse during the Famennian, when the reef ecosystem collapsed, invertebrates vanished, and only calcimicrobes played a role (Copper 1997); (4) the sharpest rise in atmospheric O_2 of the entire Phanerozoic occurred during the Late Devonian (Berner 1994, 1997). It is difficult to imagine a global atmospheric scenario in which temperatures would rise alongside an icehouse oxygen increase; (5) a warm Famennian would not explain the major Regressive–Transgressive cycles plotted by Johnson & Klapper (1992), unless such rhythmic cycles were explicable tectonically as cyclical MORBs, basalt plateaus, or continental uplift; (6) in terms of late Givetian–Frasnian atrypids, transgressive pulses normally matched diversity and abundance increases, while regressive episodes were characterised by taxa losses and extinctions (see also Day 1998). This is difficult to reconcile with transgressive pulses causing pelagic extinctions in the KW events, unless the pelagic and neritic environments were somehow decoupled, and suggests that transgressions were not related to terminal atrypid (and pentamerid) extinction towards the F-F boundary.

Anoxia and hypoxia. — A number of researchers have suggested that the F-F extinctions, as well as reef losses, were due to oxygen starvation, either from hypoxia, i.e. low levels of oxygen, or anoxia, a total lack of oxygen: this view is based on the presence of black limestones or shales (commonly referred to as the KWs, Kellwasser limestones) located near, or at the top of the Frasnian succession in Germany, Belgium and the Montagne Noire (Casier 1987; Joachimski & Buggisch 1993; Becker 1993). The same researchers favouring an anoxic hypothesis, also suggest that this is accompanied by warming. There are at least two crucial questions here. Firstly, how are black shales formed? Are they the result of anomalously high surface productivity, as suggested by Pedersen & Calvert (1990) and supported by Joachimski & Buggisch (1993) and Algeo *et al.* (1994). Or, are black shales associated with mass surface death of phytoplankton (thus anomalously low), caused by deep ocean anoxia and mass killing, and increased bottom accumulations of organic matter, the more conventional viewpoint. Goodfellow *et al.* (1988), and Wang *et al.* (1991, 1996) favoured the latter view, determining negative carbon isotope excursions at the F-F boundary, i.e. a dramatic loss of surface phytoplankton biomass. The two different interpretations lead to opposing conclusions.

The second critical question is, what drives black shale events: warming or cooling? The general interpretation, favoured by Joachimski & Buggisch (1993), Becker (1993), and Becker & House (1994), is that anoxia marks transgression, and thus warming episodes. However, modern day decadal ENSO (El Niño Southern Oscillation) events, off the west coast of the Americas, record a contrary

phenomenon: El Niño warming is driven by easterly equatorial winds, which prevent cool, nutrient-rich water upwelling from the polar regions from reaching the low latitudes (thus driving down productivity, causing the collapse of fisheries). It is the El Niños, the cold water upwellings that are the normal driving force for low latitude productivity: these are prevented by warming. Thus a highly stratified warm, transgressive ocean, typical of most of the Devonian, would not be likely to feature high surface phytoplankton productivity. But, such a stratified ocean could be readily disrupted by cooling events, bringing deep, cold, P-N rich waters to the surface, and stimulating phytoplankton-zooplankton growth (and feeding the pelagic ecosystem: today the anchovies, in the Famennian the conodonts and ammonoids). At the same time, cold waters would have a triple effect on the tropical reef ecosystem: cool water retards stenothermal reef coral metabolism, slows down or prevents $CaCO_3$ precipitation, and nutrients inhibit carbonate precipitation. Cool waters, on the other hand would stimulate the Famennian growth of cyano- and chloroxybacteria, i.e. the *Renalcis-Ephiphyton* complex typical of Famennian platforms in South China and the Canning Basin. During the Eocene–Oligocene (warm/cold) transition, productivity maxima also occurred during cold periods, with positive $\delta^{18}O$ excursions (cooling) and $\delta^{13}C$ (increasing plankton) values increasing at the boundary, accompanied by increasing ocean ventilation, and the start of the Antarctic ice sheet (Diester-Haas & Zahn 1996). This picture compares favourably with stable isotope signatures for the F-F boundary.

Organic rich black shales are best developed in cooler ocean settings, where phytoplankton productivity is increased and where greater amounts of plankton carbon are buried on the seafloor (Pedersen & Calvert 1990). Black shales thus relate more to surface productivity (and to cooling and N-P increase), than bottom anoxia. The most problematic feature of black shales and killing hypoxic events, e.g. as a cause for mass extinctions, is that there is no real proof that any correlation exists. Global supra-oceanic megaburps or megahiccups are almost impossible to visualise as killing agents because of atmospheric circulation, surface oxygen input, ocean current patterns, and the disposition of continents: the Devonian ocean probably occupied ca. 80% of the planet, and would have averaged some 4000 m depth. At best black shales tend to be localised, basinal or regional. Also, many thick Paleozoic black shale sequences are unaccompanied by global mass extinction events, e.g. the widespread late Caradoc Utica type shales of North America (reaching all the way to the Arctic), and the Ludlow black shales. The Caradoc is known as a period of increasing benthic diversity, part of the great Ordovician radiation, and, conversely, the end Ordovician mass extinction (confirmed as correlating with glaciation) rarely features any black shales in shelf settings, nor in successions where these cap reefs.

A variation of the oceanic anoxia kill model, as suggested by Wilder (1989) and Algeo (1994), propounds highly increased rates of phytoplankton production, increased chemical weathering from the first rain forests on land, and influxes of muds associated with reef termination. However, increases in oceanic phytoplankton and terrestrial rainforest would raise atmospheric levels of O_2, and increases in organic-rich shales do not necessarily imply anoxia in the underlying watermass (Pedersen & Calvert 1990). In addition, much of the black shale deposited on the North and South American cratons in the Famennian is enriched in terrestrial plant debris, logs, fresh water inverte-brates and fishes, and depreciated in normal marine invertebrates, which therefore mark shallowing estuarine coastal habitats, not deepening, and a transition to the Carboniferous coastal lowland setting. Famennian anoxia largely defines stagnant coastal environments, not flooding of continents by upwelling of CO_2-rich, offshelf waters.

Were Frasnian taxa which survived the F-F extinction events preferentially pre-adapted to living in dysaerobic habitats? If it were demonstrable that terebratulids, rhynchonellids, athyrids, spiriferids, productids and punctate orthids (the dominant Late Paleozoic surviving orders) were euryoxic, i.e. adapted to wide-ranging levels of oxygen, and that atrypids and pentamerids (two orders annihilated at the F-F boundary) were stenoxic, then a plausible argument might be made for selective extinction related to hypoxia-tolerant taxa. Unfortunately there is no such evidence. *Spinatrypa, Spinatrypina* and *Pseudoatrypa*, three of the final genera persisting in the *P. linguiformis* Zone, were common inhabitants of dysaerobic lagoonal and deep shelf settings with black shales and black micrites in the Givetian–Frasnian of North America, China and Europe. *Spinatrypina* was a keystone genus of

the *Amphipora* facies, most common in black carbonates typical of the semi-stagnant, back reef lagoons in the Givetian and Frasnian. *Amphipora* survived into the Famennian: *Spinatrypina* did not. *Iowatrypa*, another genus common in the upper *P. rhenana* and sometimes present in the *P. linguiformis* Zone, was most common in deeper water shales, and also occurred in lagoonal facies. *Invertina* from China, ancestral to *Iowatrypa*, also lived in Givetian black limestones-shales with amphiporids. Atrypids occur in the black shales of the Belgian latest Frasnian Matagne Formation: these did not survive. Thus there is every indication that although euryoxic atrypids were common in less aerobic Frasnian settings, this did nothing to assist in their survival, yet other associated taxa in these settings did survive, e.g. *Schizophoria*, and many rhynchonellids which sailed through the F-F boundary. Wide ranging, low oxygen tolerance of benthic invertebrates has not been shown to play a role in the Famennian recovery. Nor did a preference for muddy bottom substrates: atrypids were most abundant in muddy substrates throughout their history.

Transgressive–Regressive cycles

A series of Givetian–Frasnian transgressive–regressive (T-R) cycles have been plotted (Johnson & Klapper 1992), recording increasing biodiversity and abundance, and reef growth during transgressions, and extinctions during regressions (Day 1998). Veevers & Powell (1987) and Isaacson (1997) tied T-R cycles in to glacial cycles in South America; others impute no connection to climate change. It could be argued that the regressive portions of these cycles could alone drive the extinctions by decreasing shelf space, especially in the tropics and in reef habitats (the perched fauna extinction hypothesis of Johnson in 1974). Decreasing shelf space may exacerbate competition, thus reducing regional diversity. Regression is generally acknowledged as marking the very end of the Frasnian UKW event, and the beginning of the Famennian. However, sealevel drawdown may have the opposite effect: by breaking up large interior continental sealanes or basins, and separating areas formerly connected by flooding, increasing endemicity, provinciality and diversity by isolating faunas may arise. This appears evident during the Early Devonian, when overall brachiopod diversity increased during periods of relatively low sealevels and retreat of seas from continents. Possibly low Pleistocene sealevels in Indonesia increased the modern day high coral biodiversity there. Secondly, very narrow shelf areas themselves may not mean impoverished faunas: one of the most diverse modern day coral reef habitats is the Banda Islands (Indonesia), where a narrow coral reef rim 2 m wide, surrounding the active volcano Gunung Api at Bandaneira, has a stony coral fauna of 126 spp. recovering on an andesitic lava flow which smothered the reef in 1988 (Tomascik *et al.* 1996). Here high diversity appears to have been created in a very small area by a structurally complex, predator-free stable substrate, recruiting from adjacent reefs. Thus a narrow, stranded carbonate shelf may not have a significant effect on diversity: significant loss of reef area in the Pleistocene of the Pacific and Atlantic is also not believed to have played a role in decreasing Pleistocene coral diversity (Pandolfi & Jackson 1997). Budd & Johnson (1997) recorded accelerated extinction at 2.0 to 1.5 Ma, coinciding with the beginning of the Pleistocene ice ages, and noted that 75% of the 80 Caribbean Pliocene species became extinct, and more than 50% of current species originated. The Pleistocene thus marked severe turnovers, but, with high origination rates not seen in the F-F extinction events, a mass extinction cannot be postulated.

An alternative to the regression or perched fauna model as a primary cause for the F-F extinction, is that the rapidity of sealevel fluctuations itself in the Late Devonian may have been a driving factor. This would have to mean that each T-R cycle would end in extinction, and that a rate of extinction would have to be calculated for each T-R cycle, which becomes problematic. Using nektoplanktic faunas, e.g. conodonts or ammonoids, as proof for such cyclical extinctions in the pelagic setting, might end up with circular reasoning, where extinction of the very faunas used to date the zones, would also be used to identify the T-R cycles. Rapid sealevel oscillations could potentially drive extinctions, but at present proof for this is lacking and the temporal resolution to solve this problem is not at hand.

Impacts

The impact hypothesis was first promoted by McLaren (1970: p. 811), who declared as to the F-F kill causes that, 'turbid water, is therefore, my first choice', then elaborating that he would, land a large or very large meteorite in the Paleozoic Pacific at the close of the Frasnian, postulating the resulting tsunami as depositing widespread killing muds (McLaren 1970: p. 812). Impacts require proof dependent on accurate dating of an impact structure at the extinction horizon, geochemical anomalies (e.g., Pt, Ir, or PG group metals), and proof of impact sediments, e.g. tektites or fused glasses, shocked quartz. The McLaren hypothesis was followed up in the 1980s by a series of post K-T boundary papers along similar lines, outlining the F-F boundary geochemical data, but the anomalies discovered todate occur in conodont zones well above the boundary (Goodfellow *et al.* 1988; McLaren & Goodfellow 1990), or well below it (Warme & Sandberg 1996). Glassy microspherules have been found in the Famennian *crepida* zone of China, well above the F-F boundary, at roughly the same level as the *Frutexites* bed in the Canning Basin (Wang *et al.* 1992). The chief problem with single or multiple impacts in the Late Devonian, and the evidence seen in tektites or Pt-Ir anomalies, relate to timing: none are yet known to coincide with the extinctions recorded. The record of terrestrial impact cratering (Grieve 1995) shows that on average a very large impact occurs every million years, based on preservation over the last 50 Ma, but that only one, the K-T, correlates with some extinction. The Siljan crater is dated closest to the F-F boundary, with the remainder all falling within the 14–15 Ma time span of the Givetian–Frasnian (Charlevoix, Flynn Creek, Slate Islands, Ternovka, and Alamo). The Alamo crater in Nevada is early Frasnian in age, marked by shocked quartz and an Ir anomaly, but has no accompanying extinctions (Warme & Sandberg 1996). Thus the impact hypothesis has been considerably weakened.

Conclusions

Atrypid extinctions and originations in the Frasnian provide some clues to the severity, timing and causes of the F-F extinctions. The data are by no means complete, and remain contentious, and open to debate. They do not support instantaneous loss of a richly diverse and abundant biota at the F-F boundary, but match the decline of reefs below the boundary, i.e. protracted and widespread, similar to that seen at the K-T boundary, which marked a switch from Mesozoic hothouse to Cenozoic icehouse climates (Kauffman & Johnson 1997). Atrypid losses appear unrelated to anoxia, similar to the data observed for benthic ostracodes. The extinction-origination patterns, biogeography, and paleoecology of the tropically confined order Atrypida support arguments for cooling events and regressions as being primary agents for the F-F extinction.

References

Algeo, T.J., Berner, R.A., Maynard, J.B., & Scheckler, S.E. 1995. Late Devonian oceanic anoxic events and biotic crises: rooted in the evolution of vascular plants? — *GSA Today* 5, 63–66.

Baliński, A. 1996. Frasnian-Famennian brachiopod faunal extinction dynamics: an example from southern Poland. *In:* P. Copper & J. Jin (eds), *Brachiopods,* 319–324, Balkema Press, Rotterdam.

Barrett, S.F. & Isaacson, P.E. 1989. Devonian paleogeography of South America. — *Canadian Society of Petroleum Geologists. Memoir* 14, 655–667.

Beck, J.W., Recy, J., Taylor, F., Edwards, R.L., & Cabioch, G. 1997. Abrupt changes in early Holocene tropical sea surface temperatures derived from coral records. — *Nature* 385, 705–707.

Becker, T. 1993. Anoxia, eustatic changes, and Upper Devonian to lowermost Carboniferous global ammonoid diversity. — *Systematics Association Special Volume* 47, 115–163.

Becker, T. & House, M.R. 1994. Kellwasser events and goniatite successions in the Devonian of the Montagne Noire, with comments on possible causations. — *Courier Forschungsinstitut Senckenberg* **169**, 45–77.

Berner, R.A. 1994. Geocarb II: a revised model of atmospheric CO_2 over Phanerozoic time. — *American Journal of Science* **294**, 56–91.

Berner, R.A. 1997. The rise of land plants and their effect on weathering and atmospheric CO_2. — *Science* **276**, 544–545.

Boucot, A.J., Johnson, J.G., & Talent, J.A. 1969. Early Devonian brachiopod zoogeography. — *Geological Society of America Special Paper* **119**, 1–106.

Brand, U. 1989. Global climatic changes during the Devonian–Mississippian: stable isotope biogeochemistry of brachiopods. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **75**, 311–329.

Brown, B. 1997. Coral bleaching: causes and consequences. — *Proceedings of the 8th International Coral Reef Symposium, Panama* **1**, 65–74.

Budd, A.F. & Johnson, K.G. 1997. Coral reef community dynamics over 8 million years of evolutionary time: stasis and turnover. — *Proceedings of the 8th International Coral Reef Symposium, Panama* **1**, 423–428.

Buddemeier, R.W. & Fautin, D.G. 1993. Coral bleaching as an adaptive mechanism – a testable hypothesis. — *Bioscience* **43**, 320–326.

Buggisch, W. 1991. The global Frasnian-Famennian 'Kellwasser event'. — *Geologische Rundschau* **80**, 49–72

Caputo, M.V. 1985. Late Devonian glaciation in South America. — *Palaeogeography, Palaeoclimatology, Palaeoecology* **51**, 291–317.

Caputo, M.V. & Crowell, J.C. 1985. Migration of glacial centres across Gondwana during the Paleozoic Era. — *Bulletin of the Geological Society of America* **96**, 1020–1036.

Casier, J.G. 1987. Étude biostratigraphique et paléoécologique des ostracodes du récif marbre rouge du Hautmont Vodelée. — *Revue Paléobiologie* **6**, 193–204.

Casier, J.G. 1992. Description et étude des ostracodes de deux tranchées traversant la limite historique Frasnian-Famennien dans la localité-type. — *Bulletin de l'Institut Royal des Sciences Naturelles, Sciences de la Terre* **62**, 109–119.

Casier, J.G. & Develeeschouwer, X. 1995. Arguments (ostracodes) pour une régression culminant proximité de la limite Frasnien–Famennien Sinsin. — *Bulletin de l'Institut Royal des Sciences Naturelles Belgique, Sciences de la Terre* **65**, 51–68.

Casier, J.G. & Lethiers, F. 1997. Ostracodes and the Late Devonian mass extinction: Steinbruch Schmidt (Germany) and Devil's Gate (Nevada).—*Abstracts of the Geological Society of America, Annual Meeting, Salt Lake City* **1997**, 95.

Copper, P. 1975. Cold water faunas of Brazil and the Frasnian-Famennian extinction. *Abstracts Annual Meeeting Geological Society of America, Toronto*, p. 56.

Copper, P. 1977. Paleolatitudes in the Devonian of Brazil and the Frasnian-Famennian mass extinction. —*Palaeogeography, Palaeoclimatology, Palaeoecology* **21**, 165–207.

Copper, P. 1984. Cold water oceans and the Frasnian-Famennian extinction crises. — *Abstracts of the Geological Society America NE Section, Rhode Island* **16**, 10.

Copper, P. 1986. Frasnian-Famennian mass extinctions and cold water oceans. — *Geology* **14**, 835–838.

Copper, P. 1997. Reefs and carbonate productivity: Cambrian through Devonian. — *Proceedings of the 8th International Coral Reef Symposium, Panama* **2**, 1623–1630.

Day, J. 1998. Distribution of latest Givetian–Frasnian Atrypida (Brachiopoda) in central and western North America. — *Acta Palaeontologica Polonica* **43**, 205–240.

Diester-Haas, L. & Zahn, R. 1996. Eocene–Oligocene transition in the Southern Ocean: history of water mass circulation and biological productivity. — *Geology* **24**, 163–166.

Dreesen, R., Kasig, W., Paproth E, & Wilder, H. 1985. Recent investigations within the Devonian and Carboniferous north and south of the Stavelot-Venn Massif. — *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **171**, 237–265.

Erwin, D.H. 1993. *The Great Paleozoic Crisis: Life and Death in the Permian*. 327 pp. Columbia University Press, New York.

Eyles, N. 1993. Earth's glacial record and its tectonic setting. — *Earth Science Reviews* **35**, 1–248.

Feist, R. 1991. The Late Devonian trilobite crises. — *Historical Biology* **5**, 197–214.

Franois, R., Altabet, M.A., Yu, E.F., Sigmans, D.M., Bacon, M.P., Frank, M., Bohrmann, G., Bareille, G., & Labeyrie, L.D. 1997. Contribution of Southern Ocean surface-water stratification to low atmospheric CO_2 concentrations during the last glacial period. — *Nature* **389**, 929–935.

Glynn, P.W. 1993. Coral reef bleaching – ecological perspectives. — *Coral Reefs* **12**, 1–17.

Glynn, P.W. & D'Croz, L. 1990. Experimental evidence for high temperature stress as the cause of El Niño – coincident coral mortality. — *Coral Reefs* **8**, 181–191.

Godefroid, J. & Helsen, S. 1998. The last Frasnian Atrypida (Brachiopoda) in southern Belgium. — *Acta Palaeontologica Polonica* **43**, 241–272.

Goodfellow, W., Geldsetzer H.H.J., McLaren D.J., Orchard, M.J., & Klapper, G. 1988. The Frasnian-Famennian extinction: current results and possible causes. — *Canadian Society of Petroleum Geologists. Memoir* **13**, 9–21.

Grader, G.W. & Isaacson, P.E. 1997. Late Devonian paleogeography, eustatic sea-level changes and antecedent channel sandstones, central Idaho. — *Abstracts of the Geological Society of America, Annual Meeting, Salt Lake City* **1997**, 41.

Grieve, R., Rupert, J., Smith, J., & Therriault, A. 1995. The record of terrestrial impact cratering. — *GSA Today* **5**, 189, 190–196.

Guilderson, T.P., Fairbanks, R.G., & Rubenstone, J.L. 1994. Tropical temperature variations since 20,000 years ago: modulating interhemispheric climate change. — *Science* **263**, 663–665.

Hubell, S.P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rainforests and coral reefs. — *Proceedings of the 8th International Coral Reef Symposium, Panama* **1**, 33–42.

Isaacson, P.E. & Sablock, P.E. 1989. Devonian System in Bolivia, Peru and northern Chile. — *Canadian Society of Petroleum Geologists. Memoir* **14**, 719–728.

Isaacson, P.E. 1993. Devonian Brachiopoda of Bolivia. *In:* R. Suarez-Sorico (ed.), Fosiles y Facies de Bolivia. — *Revista Tecnica de YPFB* **2**, 5–33.

Isaacson, P.E. 1997. Late Devonian (Famennian) glaciation in Gondwana and forced marine regression in North America. — *Abstracts of the Geological Society of America, Annual Meeting, Salt Lake City* **1997**, 41.

Isaacson, P.E. & Grader, G.W. 1997. Late Devonian paleogeography, eustatic sealevel changes, and antecedent channel sandstones, central Idaho. — *Abstracts of the Geological Society of America, Annual Meeting, Salt Lake City* **1997**, 41.

Jablonski, D. 1989. The biology of mass extinction: a paleontological view. *In:* W.G. Chaloner & A. Hallam (eds), Evolution and extinction. — *Philosophical Transactions of the Royal Society of London B* **325**, 357–368.

Johnson, J.G. 1974. Extinction of perched faunas. — *Geology* **2**, 479–482.

Johnson, J.G. & Klapper, G. 1992. North American mid-continent T/R cycles. — *Oklahoma Geological Survey Bulletin* **96**, 567–587.

Joachimski, M.M. & Buggisch, W. 1993. Anoxic events in the late Frasnian – causes of the Frasnian-Famennian faunal crisis. — *Geology* **21**, 675–678.

Kauffman, E.G. & Harries, P.J. 1996. The importance of crisis progenitors in recovery from mass extinction. *In:* M.B. Hart (ed.), Biotic Recovery from Mass Extinction Events. — *Geological Society Special Publications* **1023**, 15–39.

Kauffman, E.G. & Johnson, C.C. 1997. Ecological evolution of Jurassic–Cretaceous reefs. — *Proceedings of the 8th International Coral Reef Symposium, Panama* **2**, 1669–1680.

Klapper. G., Feist, R., Becker, R.T., & House, M.R. 1993. Definition of the Frasnian-Famennian stage boundary. — *Episodes* **16**, 433–440.

Lethiers, F. & Casier, J.G. 1994. Les ostracodes survivants l'événement F-F dans le limitotype de Coumiac (France). — *Annales de la Société Géologique de Belgique* **117**, 137–154.

Linsley, B.K. 1996. Oxygen-isotope record of sea level and climate variations in the Sulu Sea over the past 150,000 years. — *Nature* **380**, 234–237.

Martinez, E.D. & Isaacson, P.E. 1996. Late Devonian glacially-influenced marine sedimentation in western Gondwana: the Cumana Formation, Altiplano, Bolivia. — *Canadian Society of Petroleum Geologists. Memoir* **17**, 511–522.

McGhee, G.R. 1982. The Frasnian-Famennian extinction event. — *Geological Society of America Special Paper* **190**, 491–500.

McGhee, G.R. 1996. *The Late Devonian Mass Extinction: the Frasnian/Famennian Crisis.* 303 pp. Columbia University Press.

McLaren, D.J. 1970. Presidental address: time, life and boundaries. — *Journal of Paleontology* **44**, 801–815.

McLaren, D.J. & Goodfellow, W. 1990. Geological and biological consequences of giant impacts. — *Annual review of Earth and Planetary Sciences* **18**, 123–171.

Oliver, W.A. & Pedder, A.E.H. 1994. Crises in the Devonian history of rugose corals. — *Paleobiology* **20**, 178–190.

Pandolfi, J.M. & Jackson, J.B.C. 1997. The maintenance of diversity on coral reefs: examples from the fossil record. — *Proceedings of the 8th International Coral Reef Symposium, Panama* **1**, 397–404.

Racki, G. 1998. The Frasnian-Famennian brachiopod extinction events: A preliminary review. — *Acta Palaeontologica Polonica* **43**, 395–411.

Racki, G. & Baliński, A. 1998. Late Frasnian Atrypida (Brachiopoda) from Poland and the Frasnian-Famennian biotic crisis. — *Acta Palaeontologica Polonica* **43**, 273–304.

Retallack, G.J. 1997. Early forest soils and their role in Devonian global change. — *Science* **276**, 583–585.

Rzhonsnitskaya, M.A. (Ržonsnickaâ, M.A.), Yudina, Y.A. (Ûdina, Û.A.), & Sokiran, E.V. 1997. Development of Pseudogruenewaldtinae during the final stage of atrypid existence. *In:* Problems of the systematiks and evolusion of the organic world [in Russian]. *Tezisy Dokladov XLIII Sessii Paleontogičeskogo Obsestva, St. Petersburg,* 57–59.

Sheridan, R.E. 1987. Pulsation tectonics as the control of long term stratigraphic cycles. — *Paleoceanography* **2**, 97–118.

Sorauf, J. & Pedder, A.E.H. 1986. Late Devonian corals and the Frasnian-Famennian crisis. — *Canadian Journal of Earth Sciences* **23**, 1265–1287.

Stanley, S.M. 1987. *Extinction.* 242 pp. W.H. Freeman & Co., San Francisco.

Stearn, C.W. 1987. Effect of the Frasnian-Famennian extinction on the stromatoporoids. — *Geology* **15**, 677–679.

Tomascik, T., van Woesik, R., & Mah, A.J. 1996. Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. — *Coral Reefs* **15**, 169–175.

Veevers, J.J. & Powell, C.M. 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive-regressive depositonal sequences in Euramerica. — *Bulletin of the Geological Society of America* **98**, 475–487.

Veron, J.E.N. 1995. *Corals in Space and Time.* 321 pp. Comstock Cornell Press, Ithaca & London.

Wang, K. 1992. Glassy microspherules (microtektites) from an Upper Devonian limestone. — *Science* **256**, 1547–1550.

Wang, K., Orth, C.J., Attrep, M., Chatterton, B.D.E., Hou, H.F., & Geldsetzer, H.H.J. 1991. Geochemical evidence for a catastrophic event at the Frasnian/Famennian boundary in South China. — *Geology* **19**, 776–779.

Wang, K., Geldsetzer, H.H.J., Goodfellow, W.D., & Krouse, H.R. 1996. Carbon and sulfur isotope anomalies across the Frasnian-Famennian extinction boundary. — *Geology* **24**, 187–191.

Warme, J.E. & Sandberg, C.A. 1996. Alamo megabreccia: record of a Late Devonian impact in southern Nevada. — *GSA Today* **6**, 1–7.

Webb, R.S., Rind, D.H., Lehmann, S.J., Helay, R.J., & Sigman, D. 1997. Influence of ocean heat transport on the climate of the Last Glacial Maximum. — *Nature* **385**, 695–699.

Wilder, H. 1989. Neue Ergebnisse zum oberdevonischen Riffsterben am Nordrand des mitteleuropäischen Variscikums. — *Fortschritte in der Geologie von Rheinland und Westfalen* **35**, 57–74.