

## *Megareefs in Middle Devonian supergreenhouse climates*

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### ABSTRACT

A newly refined reef database, modified to calculate reef tracts in relation to major tectonic plates, and with new paleogeographic maps, indicates that the largest known, and latitudinally most widespread Phanerozoic reefs developed during the Middle Paleozoic (Siluro-Devonian), with an acme in the Middle Devonian. Expanding during times of exceptional sea-level highstands and widespread epicontinental shallow seas, this 26 m.y. long acme of coral-sponge reef growth coincided with the warmest global temperatures known for the Phanerozoic, i.e., with a “supergreenhouse” climate mode well above Holocene interglacial norms. During the Middle Paleozoic, reefs were particularly abundant, occupying large, continental seaboard, carbonate platforms, and vast inland epicontinental seas. Examples of such “extremes” occurred mostly on passive margin settings, and extensive flooded continental interiors, e.g., the 1700–3000 km long tracts of the Western Canada Sedimentary Basin, Canadian arctic (Innuitian platform), eastern Laurentia “Old Red Continent” (United Kingdom to Poland), eastern Russian Platform (northeast Laurentia), Ural “Fold Belt” (eastern slopes of Urals), Siberia, northwest Africa, and South China. Smaller scale reef belts between 700 and 1300 km long were constructed on isolated tectonic terranes facing Gondwana on the north (Pyrenees, Afghanistan-Pakistan), Mongolia, Kolyma-Chukot, and North China. Large basins and flooded shelf areas, and the reefs featured within them, were not persistently developed throughout the Middle Paleozoic. They especially characterized the middle Emsian through Givetian (late Early Devonian–Middle Devonian). The following Frasnian (Late Devonian) showed more restricted and confined distribution of coral-stromatoporoid reefs, and during the Famennian, coral-stromatoporoid reefs “crashed” and were replaced by calcimicrobial reefs and platforms. During the latter phases of the Frasnian/Famennian mass extinctions, such microbial reefs were confined to relatively small areas, and metazoan reefs were nearly entirely obliterated, being confined to rare stromatoporoid patch reefs or lithistid mounds. Coral reefs were completely absent during the 21 m.y. long Famennian interval, and no real recovery of “keystone” frame-building, colonial corals took place in reef settings. The Famennian coincided with repeated glaciations, sharp sea-surface cooling events, sea-level drawdowns, and concurrent, matching stable isotope excursions.

**Keywords:** Phanerozoic acme, Middle Devonian, coral-sponge reefs, supergreenhouse climates.

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## INTRODUCTION

The Holocene is an unusual episode in Phanerozoic Earth history with respect to reef distribution worldwide, as well as its climate fluctuations between glacial and interglacial intervals. There are three relatively large, continuous, barrier reef platforms today with prolific coral growth: (1) the Great Barrier Reef, which is about 2100 km long stretched along the east coast of Australia to New Guinea, (2) the shelf along New Caledonia, which is 750 km long, and (3) the Yucatan shelf, which is 650 km long. Only the Great Barrier Reef can match some of the much larger scale reefs of the Devonian reef optimum, and thus the Holocene cannot be considered to have typical large-scale barrier reef development for the Phanerozoic, the past 544 m.y. of Earth history. This can most likely be attributed to the fact that for most of post-Cretaceous time, Earth has been in an icehouse mode, oscillating around cool episodes defined by bipolar glaciation. Holocene reefs of the present interglacial warm episode, the past 12,000 years, are normally confined to tropical low latitudes roughly below 27°N and S on eastern seaboards (Wells, 1988; Veron, 2000). Reefs occur at higher latitudes on the eastern seaboards because they are influenced by warm currents, e.g., Bermuda 32°25'N (generated by the Gulf Stream), Gulf of Aqaba 29°30'N (Wells, 1988), Sea of Japan at Iki Island 34°N (Yamano et al., 2001), and Lord Howe Island, Australia, 31°30'S (Veron, 2000). The southernmost west Australian reefs, the Houtman Abrolhos, occur at 29°S, while on the Australian east coast, the most southerly reefs occur near Brisbane at 27°S (Veron, 2000). Reefs in the Gulf of Aqaba are sustained at relatively high latitudes because of minor riverine input and very clear waters, despite sporadic cool winter temperatures. Reefs on the east African coast range to latitudes between 26° and 27°S (Veron, 2000). Shallow water coral communities (biostromes) with reasonably dense stands of low diversity corals may occur at even higher latitudes than reefs.

On the western sides of continents, due to cold currents and nutrient upwelling, Holocene reefs are unknown at latitudes higher than 10°N and S. On the west coast of Africa there are only coral thickets, and zooxanthellate hermatypic corals are restricted to waters less than 20 m deep (Wells, 1988). As for much of the eastern coastline of Brazil affected by the Amazon drainage (where the southernmost Abrolhos reefs are located at 18°S), a secondary constraint for west African reefs is high river runoff with low salinities, and high rates of sediment influx. These relatively low latitude modern reef distribution patterns are not the norm for most of the Phanerozoic, except for the cooler Late Paleozoic, the Early Triassic, and much of the Cenozoic (but for the late Paleocene and Eocene warm episodes). Despite an improved database (Kiessling et al., 1999; Kiessling, 2001), the reef picture resolution is still relatively coarse and insufficient for producing complete global maps at the stage level or less. In other words, the fossil reef database lacks the precision of the 5 m.y. long Pliocene-Quaternary reef database that has been accumulated over the past 50 years. Several reasons for this bias

are evident: (1) large carbonate platforms have disappeared via uplift and erosion or subduction (e.g., Tibet, eastern Australia); (2) little is known about the very small, but widespread, fringing reefs on ancient island arcs and atolls (one of the chief types of modern reefs so well known to Darwin); (3) largely unexplored subsurface drill core data exist in remote areas; and (4) many carbonate platforms are simply inadequately described, or little known, in a modern carbonate sedimentology sense, e.g., Mongolia, Tian Shan, North China, and northeastern Russia. Thus, at best, our database remains only preliminary. Often the information that is published is controversial, with some authors interpreting the distribution of reefs in terms of present-day environments. (e.g., James and Bourque, 1992; Copper, 2001), and others promoting ideas suggesting that (1) Phanerozoic reef distribution is either unrelated to latitudinal dispersal or to temperature (Kiessling, 2001); (2) that ancient reefs have no, or few, modern analogues, and therefore do not fit actualistic patterns (Wood, 1999); or (3) that modern Cenozoic reefs have entirely different modes of skeletonization favoring aragonite supersaturation, and thus show temperature and carbon dioxide solubility constraints, or responses, that are diametrically opposed to those of the dominant Middle Paleozoic calcite ocean mode (Kleypas et al., 1998).

Reefs are herein defined as three-dimensional, biogenic, carbonate structures raised above the surrounding seafloor, generally possessing a fringing apron of reef-derived flank deposits. Reefs are defined sedimentologically by massive bedding in the reef core, usually a skeletal, reef-builder framework (e.g., calcimicrobes, algae, sponges), but also carbonate muds, producing fluid-conducting cavities and containing carbonate cement. In this we, therefore, include the spectrum of mudmounds, following Wood (2001). The term tropical, as used in this paper, does not strictly refer to the modern region between the tropics of Cancer and Capricorn, 23°28'N and S. Purely artificial latitudinal constraints do not adequately describe the distribution of warm marine environments during greenhouse modes more typical of much of the Phanerozoic. The marine tropics are herein defined by climate and temperature constraints, i.e., as marking the limits of vigorous coral skeleton growth (and CaCO<sub>3</sub> sponge skeletons) in shallow waters where the sea surface/atmosphere interface never drops below freezing. In a supergreenhouse, Middle Paleozoic world (Berner, 1997), the tropics expanded poleward, with average global temperatures 4–14 °C above the Holocene average of 16 °C. Thus, it is not only the mean tropical sea-surface temperature that provides the constraint to reefs, but also the annual maximal and minimal temperature, much as most human agriculture is constrained by the onset of winter frost during harvest, or late frosts for seeding in spring. On land, the comparable tropical climate belt would be defined by the limit of normal, humid tropical plant growth and reproduction, e.g., palms, coconuts, mangroves, etc.

A further latitudinal constraint for modern reefs may be cyclical, indiscriminate bleaching events, such as those that accompanied the 1997–1998 El Niño (Wilkinson, 2000), though

the fossil record for bleaching, and coral reef recovery therefrom, remains very uncertain. This means that tropical metazoan reefs of the Middle Paleozoic could move to as high as the 40° to 50°, and possibly 60°, latitudes. Such an extended range for reef occurrences fits well with paleogeographic maps of the Middle Devonian presented in this paper (Fig. 1). Broad patterns and regionally detailed surveys of the distribution of Emsian through Givetian reefs, their thickness and broad faunal construction, are now extractable from our own database. This paper updates the distribution of Emsian through Givetian reefs in a plate tectonic framework, i.e., as Devonian carbonate platforms or island arc belts flanking major plates (see also Scotese, 2001; Copper, 2002). We have broadly defined the term *reef tracts* as large, carbonate platforms in which reefs are a common, and more or less continuous, though not an evenly distributed feature. This thereby also includes “Great Barrier Reef” tract types (GBRs), epicontinental seas dominated by large or small patch reef complexes, tectonically isolated Bahama-type platforms, or the narrower platforms of chains of fringing reefs around tectonically active island arcs, or collisional plate margins with fringing reefs.

### DEVONIAN (EMSIAN-GIVETIAN) REEFS

During the beginning of Early Devonian time (Lochkovian-Pragian), reef development was generally constricted worldwide due to relative sea-level lowstands and limited accommodation space (Copper, 2002). However, during the succeeding Emsian, reef expansion was rapid. There are at least three major and divergent paleogeographic reconstructions for the Emsian through Givetian (late Early Devonian–Middle Devonian). These include: (1) a Laurentia-centric version, in which the dominant reef growth patterns encircle Laurentia, and in which collision between

Laurentia and western North Africa is shown to have taken place by the Gedinian (Golonka et al., 1994; Kiessling et al., 1999; Scotese, 2001), (2) a version centered around Russia-Siberia-Kazakhstan with major reef belts in the 5–20° latitudes north (Zonenshain et al., 1990a, 1990b; Fig. 13 in Kuznetsov, 2000), and (3) an eastern Gondwana, Sino-Australo-centric version that places the Chinese plates proximal to Australia (Talent et al., 2000). The lengths of these reef belts varied from ~3100 km to as little as 400 km (Table 1).

These three stages of the Devonian, beginning in the latter part of the Early Devonian (middle to late Emsian), and ending in the Givetian, are broadly agreed to mark the Phanerozoic peak of reef development on a worldwide basis, with reefs reaching much higher latitudes than the Holocene climatic optimum (Copper, 1994; Kiessling et al., 1999; Kiessling, 2001; Copper, 2002). A peak in latitudinal reef distribution and in the size of carbonate platforms and epicontinental seas with reef belts was reached during the Givetian, after which there was a sharp decline and retreat of reefs from many areas, generally accompanied by sea-level draw-down; note that the reef abundance database is artificially skewed toward the Frasnian because of extensive drill core data from western Canada (Kiessling et al., 1999). However, reef development was far from uniform during the 26 m.y. long Emsian through Givetian reef optimum. A revised absolute time scale for the Devonian (Okulitch, 1999) shows that the Emsian represented 15 m.y., the Eifelian 7 m.y., and the Givetian 4 m.y. By the late Emsian, reef and peri-reefal faunas generally became very cosmopolitan, dominated by an Old World component that may be found east to west from Australia through South China, the Urals, western Europe, and northwestern Canada. Malvinokaffric cool climates centered around Gondwana (South America and southern and central Africa), were dominated by siliciclastics and lacked limestones and

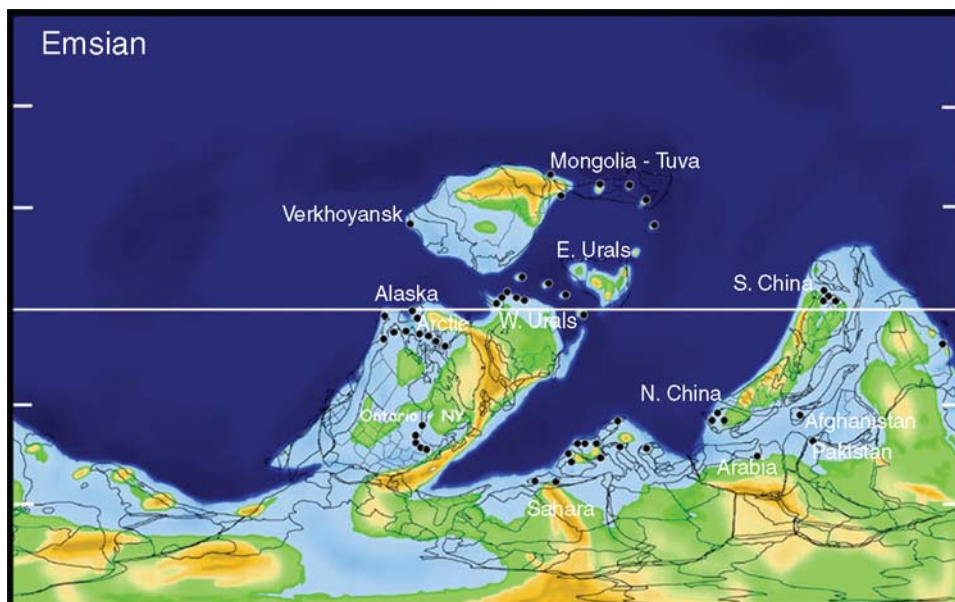


Figure 1. Plate reconstruction for the Emsian (late Early Devonian) showing initiation of Devonian reef megacycle, mostly in the middle to late Emsian. Reefs were developed in 30–35° latitudes in Mongolia-Tuva as part of active tectonic margin (see Scotese, 2001). Reefs in northern Gondwana (Morocco) grew at 45–50°S, and microplates of south European archipelago nearby, e.g., Spain, Sardinia, Carnic Alps, Montagne Noire, Barrandian high, and Armorica, at ~40–45°S. Few Emsian reefs occurred in eastern or western Laurentia, except in the Appalachian Basin and equatorial Inuitian Platform of Arctic Canada. A long belt probably developed on active eastern Australia margin, but much of this was lost by subsequent subduction of platform or erosion. Kazakhstan should have Emsian reefs (to date unreported), since reefs were developed earlier in the Lochkovian, and later in the Givetian.

TABLE 1. TOP 20 "GREAT BARRIER REEFS" OF THE EMSIAN-EIFELIAN-GIVETIAN, WITH ESTIMATED LENGTH OF THE REEF TRACT IN ROUGH ORDER OF SIZE

1.	Western Canada reef province (stable platform, western Laurentia): ~3100 km
2.	Ural fold belt (active, island arc belt): ca. 3000 km
3.	Northeast Baltica or Russian Platform (stable platform, Pechora to Volga Urals): ~2600 km
4.	Alaska-Canadian arctic (stable Inuitian platform): ~2500 km
5.	East Australia-New Guinea margin (tectonically active, ? isolated carbonate platforms): ~2000 km
6.	Near East tract (eastern Iran-Afghanistan-Pakistan): ~1900 km
7.	Southeastern Laurentia or "Old Red Continent" (Northwest Europe, United Kingdom-Poland): ca. 1800 km
8.	Mongolia-Tuva plate (southern Mongolian Gobi): ~1800 km
9.	South China plate (Vietnam-Guangxi-Hunan): ~1700 km
10.	Belarus to Caspian Basin (eastern Laurentia, stable platform, but discontinuous): ~1600 km
11.	Kazakhstan (central Kazakhstan to Junggar, Xinjiang): ~1600 km
12.	Spanish plate (Pyrenees: 800 km), or alternatively Bohemian facies tract Spain-Prague Basin, 1600 km.
13.	Siberia (southern and central): ~1500 km
14.	Saharan reef tract (Western Sahara-Morocco-Algeria): ~1200 km.
15.	Eastern Laurentia (Eifelian only: Pennsylvania-Hudson Bay): 1100 km
16.	Russian Tian Shan fold belt (Uzbekistan-Pamirs): ~1000 km.
17.	Tarim-Karakorum plate (northern flank): ~1000 km
18.	Kolyma plate: ~800 km arcuate tract
19.	North China plate: ~700 km
20.	Western Australia (Givetian, Canning Basin): ~400 km.

Note: Compare top three today: Australia-Papua New Guinea, Great Barrier Reef 2100 km, New Caledonia 750 km, Yucatan 650 km.

reefs; not even microbial mudmounds were present. The northern fringes of Gondwana, i.e., those located in the Saharan belt (Morocco-Libya), had microbial mudmounds, modest development of coral-stromatoporoid reefs and carbonate platforms, and shared some common faunas with Appalachian North America.

## REEF TRACTS AND PLATE LOCATIONS

### Laurentia (North American Plate)

There is broad agreement in terms of climate sensitive sediments, faunas, and reefs, that Laurentia straddled the equator during the Devonian, with most of the plate in the southern hemisphere (Fig. 1). The equator cut through Alaska and passed just north of Greenland. By early Emsian time, if not earlier, Baltica had fused to Laurentia. The Avalon-Meguma terrane, a rifted fragment broken from Gondwana, had probably collided in the Late Ordovician or Early Silurian, sealing off part of the Iapetus Ocean (Lin et al., 1994). The Appalachians were rising and

continued along the eastern margin of Greenland. An Arctic mountain belt arched around the north Greenland coast westward, to the northern fringe of Laurentia.

Active volcanism, and the development of large deltas in a humid tropical setting, prevented active reef development along much of the eastern margins of Laurentia in the Early-Middle Devonian, due to the Acadian orogeny in the Appalachians. However, small, isolated Lochkovian stromatoporoid and bryozoan reefs were present in the Keyser Limestone of the Appalachian Basin as far south as Tennessee (Smosna, 1988). To the northeast Gaspé, pinnacle reefs were present in the Pridolian-early Lochkovian West Point Limestone; these were associated with volcanics, but were buried by the Pragian-Emsian (Bourque and Amyot, 1989; Bourque, 2001). During the Emsian through early Eifelian, minor patch reef growth occurred in the southern Ontario Detroit River Limestone, and New York's lower Onondaga Limestone (Fagerstrom 1983; Lindemann, 1989), located at about 40°S. Onondaga pinnacle reefs occur in the subsurface of Pennsylvania (Woodrow et al., 1988). Onondaga reefs may have been inhibited by a quasi-estuarine circulation pattern, such as that seen in the Java Sea today (Edinger et al., 2002). In northern Ontario, the late Emsian, reefal Kwatabohegan Formation was capped by evaporites at 30°S (Telford, 1988). The Pennsylvania-New York through Hudson Bay Emsian reef belt probably extended along a sea lane ~1100 km long, as carbonate xenoliths in kimberlite pipes indicate that areas presently lacking Devonian strata were covered by Devonian seas (McCracken et al., 2000). On the western side of Laurentia, including the western United States and Canada, Emsian reef development was absent, and reefs were not initiated until Middle Devonian time.

The most extensive Emsian reef belt, more than 2500 km long, was wrapped around the northern margin of Laurentia, which is presently within the Canadian arctic (Fig. 1). Though its location is uncertain, the Alexander Terrane was fringed by Pragian-Emsian reefs in an outer island forearc setting (Soja, 1988: possibly an extension of the Arctic reef belt). Emsian to early Eifelian coral-stromatoporoid reefs of the Prongs Creek and Ogilvie formations in the Yukon (Perry, 1979), and in nearby eastern Alaska (Clough and Blodgett, 1988; Soja, 1988), were part of an isolated stable carbonate platform linked to the Arctic belt to the east. Along the stable carbonate shelf of the Northwest Territories, Eifelian coral patch reefs were present (Noble and Ferguson, 1971). In Arctic Canada, reefs were even more widely developed during the Emsian than in the preceding Early Devonian (Smith, 1985). This stable platform reef belt, mostly assigned to the Emsian Stuart Bay and lower Blue Fiord formations, stretched ~1600 km westward from Ellesmere Island, where ~100-m-thick patch reefs were present (Smith, 1985). The most westerly extension of this platform was at the Prince of Wales Strait, along western Victoria and Princess Royal Islands (see Fig. 2), where Emsian-Eifelian reefs of the Blue Fiord Formation reached diameters of a kilometer or more, and are exposed as prominent reef clusters for ~170 km of outcrop (Thorsteinsson and Tozer, 1962). Emsian and early Eifelian reefs

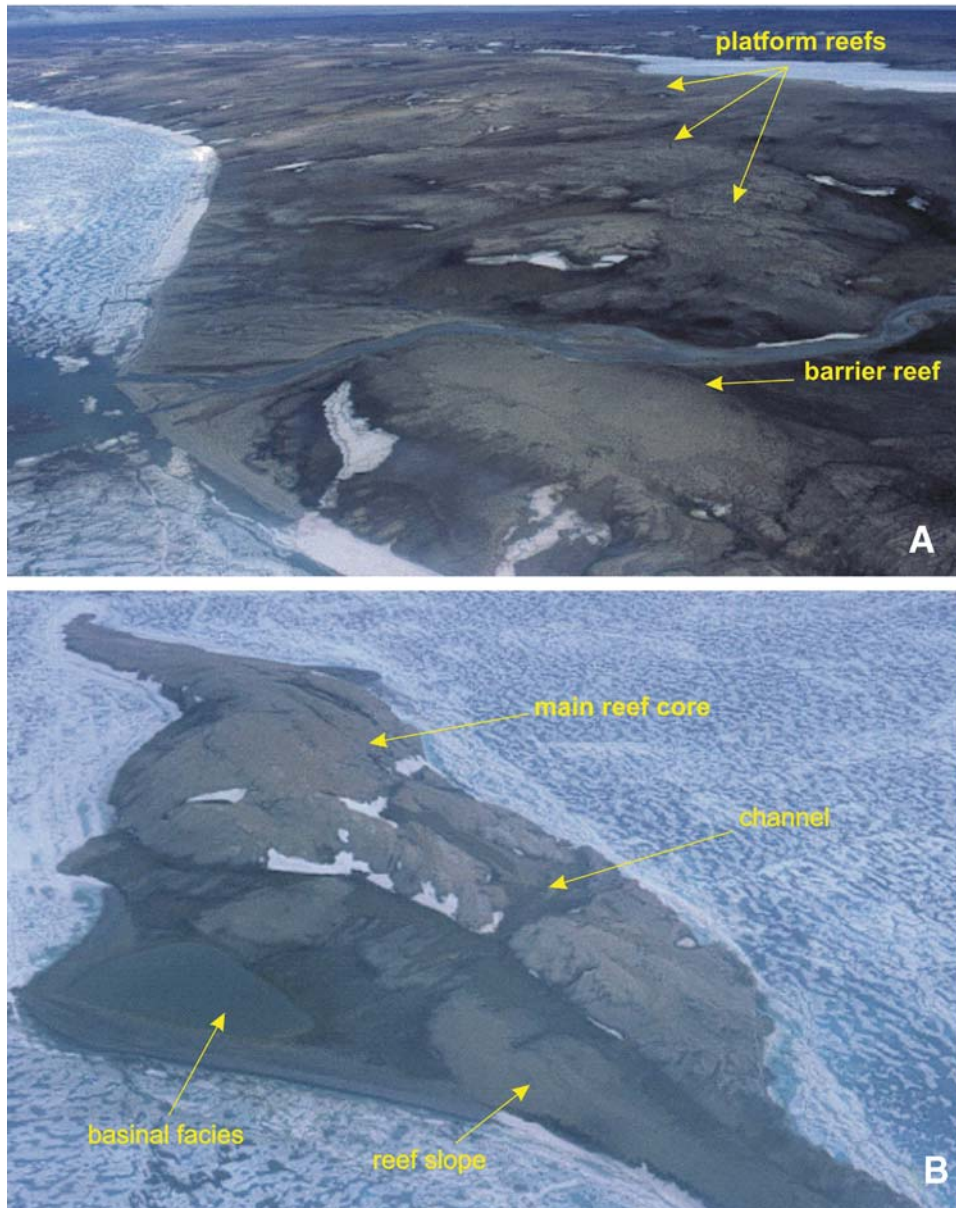


Figure 2. Two views of typical large-scale Middle Devonian reefs, part of Arctic Innuitian “Great Barrier Reef” province, which extended 2500 km from Banks and Victoria Islands, past Melville to Ellesmere Island. Part of reef belt is on western flank of Victoria Island. A: The ~150-km-long Blue Fiord Formation tectonically undisturbed reef tract with large coral patch reefs up to 1 km in diameter on the western shore of Victoria Island (Prince Albert peninsula), ~20 km north of Hay Point, ~N72°, 50′, E117°. B: view of Princess Royal Island (between Banks and Victoria Islands) reef perspective; this flat-lying coral-stromatoporoid reef portion, looking southeast, is ~2.2 km long, <1 km wide, and <50 m thick, with reef flank facies, deeper water dark grey calcareous shales, and debris flows dipping northwest, toward Banks Island (see also Thorsteinsson and Tozer, 1962), Eifelian–early Givetian, Blue Fiord Formation, Princess Royal Island, Prince of Wales Strait, at N72°45′; E118°05′. (Photos by Paul Copper.)

to the northeast of Banks Island included those on large Bahamatype carbonate platforms of Cameron and Prince Patrick Islands (Smith, 1985). These Arctic Emsian reefs were all developed within about 10° from the equator, open to eastward-flowing, warm tropical gyres.

Following deepening and extensive siliciclastic supply from the Appalachian deltas to the east, reefs were not present in the Appalachian Basin until the early Givetian, as small tabulate coral patch reefs of the Silica Shale in Ohio (Stumm, 1969). By the late Givetian, a modest return of reefs to eastern North America is marked by small, coral-capped mudmounds of the Tully Formation in New York (Heckel, 1973), and stromatoporoid-coral patch reefs of the Traverse Group in Michigan (Kesling et

al., 1974; Meyer, 1989). To the south, in Iowa and Missouri, extensive, very shallow water carbonates, frequently alternating with intertidal and evaporitic sediments, showed episodic, coral-rich biostromes, but reefs were lacking during the Eifelian-Givetian, as well as Frasnian (Witzke et al., 1988). To the northeast, reef development had ceased in the Gaspé in Quebec, Canada, before Emsian time, and no later reef developed until microbial mounds in the Carboniferous (Bourque et al., 2001).

The Middle Devonian “Great Barrier Reef” Belt of western Canada and the northwestern United States has been well documented and reviewed previously (McMillan et al., 1988; Moore, 1988, 1989). Reefs were most extensively developed in western Canada from the middle Eifelian through middle Givetian, ranging

from subsurface pinnacle reefs of the Winnipegosis Formation south of the Canadian border (Edie, 1959) to the Hume Formation on the Carnwath River, Mackenzie delta (Mackenzie, 1969), for more than 3100 km. In Eifelian time, an isolated 300-km-long reef tract was also present as far south as southern Nevada, though in the Givetian, this switched to evaporites (Johnson et al., 1991). During growth of the Givetian Keg River reefs in Alberta, on the western margin of Laurentia, inter-reef and back-reef sediments were usually organic-rich and bituminous, suggesting high rates of shelf plankton productivity, and adaptation of reef organisms to episodic hypoxia from upwelling deeper waters below the oxygen minimum zone (Chow et al., 1995). In the late Givetian, this reef belt shrank to a broad platform less than 800 km long, and about 600,000 km<sup>2</sup> in area, from the Swan Hills area of central Alberta in the south (Fischbuch, 1968) to the Great Slave Lake (Moore, 1989). Another smaller, late Givetian isolated reefal platform of the Kee Scarp Formation, <1000 km<sup>2</sup> in area, exists in the Normal Wells area (Muir et al., 1984). By the Frasnian, reefs shrank and retreated largely to central and southern Alberta; their decline was possibly related to periodic regressive cycles (Moore, 1989).

From middle Eifelian to Frasnian time, reefs almost entirely disappeared in the Canadian arctic, except for a restricted early-middle Frasnian reef platform belt on northeastern Banks Island (Embry and Klovan, 1971; Embry and Klovan, 1989; Embry, 1991). This is attributable to development of a giant siliciclastic delta wedge, derived from the northeast as far as Greenland, commencing by draping over Eifelian Blue Fiord reefs, with the delta expanding in the Frasnian to middle Famennian (Figs. 3 and 4). This clastic wedge was several kilometers thick, and more than 1.5 million km<sup>2</sup> in area, containing coal units and abundant plant remains, locally dumping fossil logs into the isolated Frasnian reef platform of northeastern Banks Island to the distal west. Embry (1991) attributed the build-up of this mega-delta to uplift, high subsidence rates, and climate change from humid to dry savanna, but episodic late Frasnian and Famennian sea-level drawdowns and cooler, drier climates may also have been important factors.

#### **Northwestern Europe (Eastern Laurentia: The “Old Red Continent”)**

On the southeastern flanks of the Old Red Continent, i.e., the areas represented today by England, northwestern France (Boulonnais), Belgium, Germany, and Poland, the Early Devonian (Emsian) was dominated by siliciclastic facies, with plant remains, fish faunas, and other evidence indicating broad coastal delta plains (Blieck et al., 1988). These were generally unsuitable for reef development until the middle to late Eifelian, though some thin coral-rich biostromal carbonates are known. Similarly, the Russian Platform and Baltic Basin, though located on the easterly tropical flank of Laurussia, were apparently unsuitable for reef growth during the Early Devonian, probably as a result of river drainage and extensive wet coastal deltaic plains, providing metaline and mud-rich shelf waters prohibitive for reefs. Such

a situation seems analogous to the easterly drainage of the Amazon River today, also in the sense that early, shrubby pteridophyte land plants were being established in such coastal areas of the Old Red Continent.

During the Eifelian, as the east and west margins of the Rheic Ocean were approaching, reef development was initiated almost the full length of the northeast-southwest-trending eastern seaboard of Laurussia, from Devon, England, through northwest France, Belgium, Germany, and Poland (~1800 km), and another 1600 km distally to the edge of the Caspian embayment. The northeast tip of this continental margin touched the equator in the Middle Devonian. Whether this was a continuous reef belt is not clear, as major gaps exist in the outcrop and possibly in the subsurface record. The shelf was narrow to the south latitudes at about 30° and widened toward the Russian Platform, flooded partly by a large, shallow, epicontinental sea. Ziegler (1982) constructed the Armorican Massif as an integral part of Laurentia, extending eastward along the plate margin toward the Saxo-Thüringian Basin and Barrandian high and separated to the south from the Montagne Noire and other plates by a long island continent, the Ligerian-Vosgian-Moldanubian cordillera (but see below where the Armorican Massif and Saxo-Thüringen belt are joined to the Southern European Archipelago). In the maps presented here (Figs. 3 and 4), Armorica is shown adjacent to the northern margin of Gondwana.

The literature of northwestern European Middle Devonian reefs is now vast: it has been reviewed by Jux (1960), Krebs (1974), Burchette (1981), and Blieck et al. (1988). The late Eifelian-Givetian represents the acme of reef development, though in some areas reefs continued well into the late Frasnian. Considerable siliciclastic influence (the “Rhenish facies”) curtailed reef development in the early and middle Eifelian, and the total pile of carbonates-siliciclastics was up to 1.5 km thick. Reefal facies in England seem to have flourished best in the late Eifelian through Givetian, as it did northwestern France, in Belgium, and east of the Rhine. In southwest England, platform margin reef facies commenced in the Givetian (Scrutton, 1977). In the Boulonnais outcrops of northern France, small patch reefs mark the Givetian Blacourt Formation (Mistiaen and Poncet, 1989). The south and west margins of Armorica (Massif Armoricain) featured coral patch reefs near Brest, Nehou, and Angers during the Pragian, but reef decline was evident in the early Emsian (Cavet et al., 1967; Poncet, 1977; Plusquellec, 1980; Morzadec et al., 1988). These were, in view of their brachiopod-coral faunas, considered to be part of the eastern proto-Atlantic south European archipelago by Hladil et al. (1999), but part of the Old Red Continent as proposed by Ziegler (1982) and Franke (1999). The Belgian mixed siliciclastic-carbonate ramp appears to have had strong sea-level and cyclonic controls restraining reef development in the Eifelian, but by Givetian time, numerous stromatoporoid, coral, and microbial reefs developed on a wide platform with back reef lagoonal facies (Préat and Weiss, 1994). Severe back-stepping of reefs in the Belgian Frasnian ultimately ended in the rapid burial of reefs by muds, silts, and sands in the late Frasnian.

In the classic Eifel region west of the Rhine, which extended as a shelf to Bergisches Land east of the Rhine for about 250 km, patch reefs were developed in a mid-to-distal, possibly outer ramp to platform margin (facies type B in Faber et al., 1977; Faber, 1980), distal to land sources of siliciclastics to the northwest. These included planar to tabular stromatoporoid reefs as well as patch reefs with abundant corals, and perireefal, biostromal communities with crinoid meadows, phaceloid and branching rugose corals, and platy tabulates. In late Eifelian time (Ahbach beds), mudmounds with coral-stromatoporoid caps

sporadically developed in the Eifel, e.g., in the Hillesheim and Dollendorf synclines (Malmsheimer et al., 1996; Pohler et al., 1999). Reef development rich in corals continued into the early Givetian (Loogh-Cürten Beds) and middle Givetian (Dreimühlen-Rodert Beds) in the same area, sometimes shallowing into intertidal facies (Birenheide et al., 1991). In the Prüm syncline, coral patch reefs up to 6 m thick and 30 m in diameter are present in the late Givetian Bolsdorf and Wallersheimer dolostones; the latter upper units are possibly of early Frasnian age (Jux, 1960). Reefs effectively ceased in the Eifel region during the Frasnian

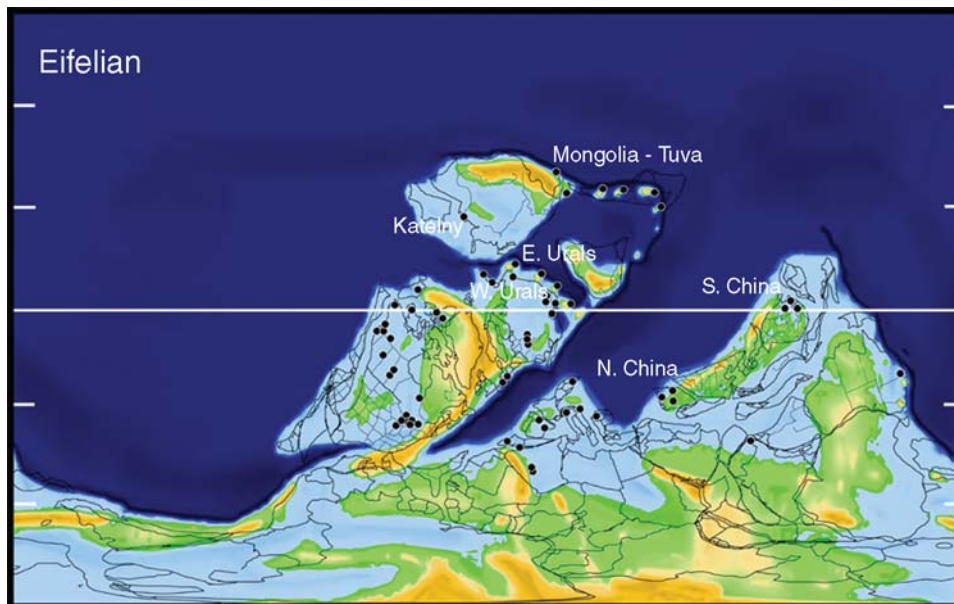


Figure 3. Plate reconstruction for Eifelian time showing a major expansion of reef belts for Middle Devonian. Reef tracts expanded considerably in western and central North America (Western Canada Sedimentary Basin), southern and east-central Laurentia (Hudson Bay and south), the east side of the Old Red Continent (i.e., platform to ramp of England through Poland), and the Russian Platform (W slope Urals) and eastern Urals. Reef growth was less extensive in areas on north margins of Gondwana (Morocco to Prague Basin). A Near Eastern reef belt stretched from Iran through Pakistan. Reefs were present on the eastern side of Kazakhstan. Reefs continued in Mongolia, Hingganling ranges of northern China, and Amur region.

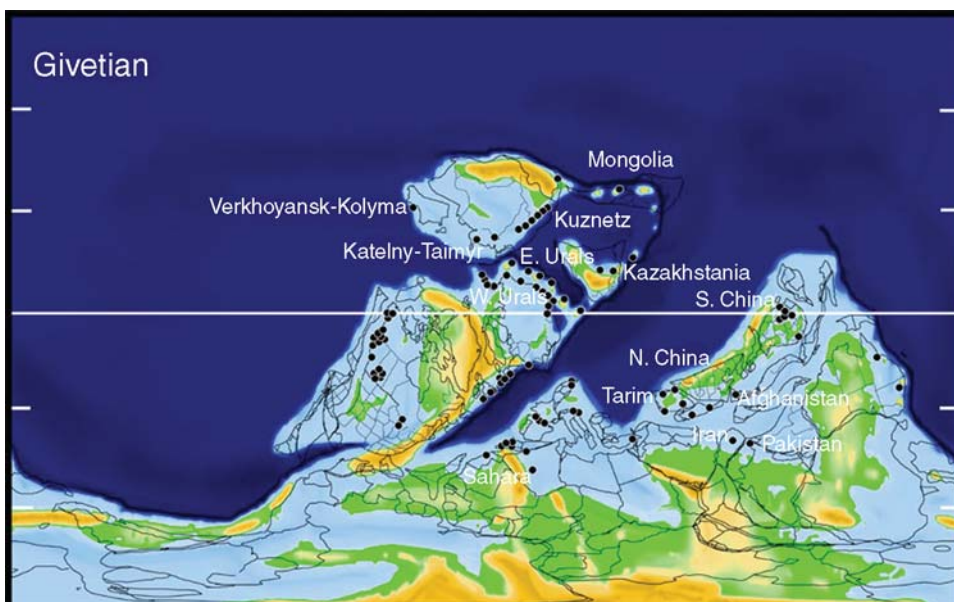


Figure 4. Maximal expression of Devonian (Givetian) saw widespread barrier reef provinces and high-latitude reef growth. Marine barrier between Laurentia and Gondwana had narrowed to a shallow seaway less than 500 km wide. At least eight or nine giant barrier reef provinces, greater in length than, or comparable to, the Holocene Great Barrier Reef of Australia were present (see Table 1): (1) northwest Gondwana (Morocco-Pyrenees); (2) England-Poland on eastern Old Red Continent; (3) western Canada; (4) central to north Urals (both on stable platform of east Baltica and the offshore, island arc Urals); (5) Siberia and northeast Russia (Kolyma-Verkhoyan); (6) Tarim-Afghanistan; and (7) south China and proximal areas of Vietnam, Laos, Cambodia, and Thailand.

and were succeeded by intertidal micritic facies, or black shales rich in goniatites.

East of the Rhine, small patch reefs of middle Eifelian age first occur in the Hobracker Formation (Scheibe, 1965) and continued into the late Eifelian Honsel Formation (Scheibe, 1965; Buggisch and Flügel, 1992; Malmshemer et al., 1996). Givetian reef development varied in different basins east of the Rhine (May, 1983, 1994). To the north, the stable shelf featured stromatoporoid reef facies at the deeper part of the shelf margin (May, 1997), though Machel and Hunter (1994) favored interpretation of the Massenkalk as a wave-resistant barrier reef like the Great Barrier Reef of Australia. In the basinal facies, reefs beginning in the Givetian *varcus* zone had regional tectonic controls and were commonly associated with local volcanic highs or “Schwellen” (Königshof et al., 1991; Weller, 1991; Buggisch and Flügel, 1992; Braun et al., 1994; Braun and Königshof, 1997). The Lahn syncline, part of the Rhenohercynian fold belt, could be viewed as developing in a backarc basin parallel to the Old Red Continent stable platform reef carbonates, which ranged from the Eifel west of the Rhine some 250 km through Brilon, east of the Rhine. Alternative views consider the Rhenohercynian massifs to be part of microplates flanking other Gondwana terranes to the south; see below. The Massenkalk reef facies continued into the early Frasnian, possibly with a break, but it was ultimately disrupted by deposition of the organic-rich Kellwasser limestones. For Poland, following Eifelian evaporites, an extensive Givetian reef platform with coral-rich shoals and coral banks was constructed, but reefs also developed on a reduced platform later in the Frasnian (Racki, 1988; 1992).

### Russian Platform (NE Laurussia)

On the western side of the Russian platform, a Middle Devonian carbonate platform with reefs ~400 km wide occurs in the subsurface of Belarus (Makhnach et al., 1986); this was apparently a carbonate platform isolated from the Polish reefs to the west. The Pripyat-Donets Graben (aulacogen), to the southeast of Belarus, was not opened to reef development until Late Devonian time (Ioganson, 1990d). Farther on the eastern flanks of Baltica is the large, subcircular Caspian Basin, flanked by a rim of Devonian reefs of Eifelian-Givetian age (the “Precaspian syncline” of Rusetskaya and Yaroshenko, 1990, or the Caspian Basin of others), located at the paleo-equator. This ~400,000 km<sup>2</sup> region represents the buried southeastern, stable flank of the Baltica plate, with drillcore data revealing coral-stromatoporoid reefs from a few meters in thickness and diameter to structures 150 m thick and over 1 km in diameter. Late Devonian (Famennian) microbial reefs, part of the north Caspian Basin, are known in drillcore from the northeast corner of the Caspian Sea in western Kazakhstan, just as they were located on a rimmed carbonate platform in the Karatau ranges to the east (Cook et al., 1994). This subsurface Devonian Caspian reefal complex on the southeast corner of Baltica ranged past Ufa for ~1000 km northward as the Volga-Ural Basin, though generally to the north, the Middle Devonian

turned to siliciclastics, and the Frasnian contained barrier reefs, atolls, and isolated reef platforms separated or underlain by black Domanik limestone facies (Ulmishek, 1988; Rusetskaya and Yaroshenko, 1990). Kirikov (1988, p. 522) described the south-east Russian platform (the “Kama-Kinel trough”) with “barrier-type [reefs] extending for hundreds of kilometers...and a width of no more than 15 km...dominated by algal limestone” during the Frasnian, and continuing into the Famennian. The stable shelf of northeastern Baltica in the Timan-Pechora region shows mostly dolomitized, platform-edge Frasnian reefs in the subsurface and outcrop (Grachevskii and Solomatin, 1977; Belyaeva, 1986). These are similar to and slightly separated from those of the Caspian Basin and Volga-Ural parts of the Russian Platform to the south (Ulmishek, 1988). If the reef belt from Pechora is connected to the Caspian basin, this stable carbonate platform on the northeast margins of Baltica, at ~2600 km long, would be the second longest reef tract of Russia.

### Eastern Slopes of the Urals (Active, Unstable Margin, Island Arcs)

The “Uralian reef province” on the northeast margin of Laurussia or Euramerica (Figs. 3–5) is usually shown as two separate tectonic units: (1) the western slopes, part of the stable platform and eastern shelf of Baltica, from the Pechora region southward (Laurussia or Euramerica: see above paragraph), and (2) the unstable island arc complexes on the eastern slopes of the Urals (the Ural fold belt). These long, parallel carbonate belts developed Middle and Upper Devonian reefs, though many were concentrated in the Late Devonian (Sokolov, 1986). Zonenshain et al. (1990a) identified the eastern Ural reef belt oriented in a more or less east-west alignment as flanking the north side of the Baltica plate or Russian Platform in the Lower and Middle Devonian. This is the longest and most extensive Devonian reef belt of Russia, developing almost continuously, with some breaks, from the Late Silurian into the Late Devonian over more than 3000 km from the southern end of the Urals to northern Novaya Zemlya (Zadoroshnaya et al., 1990a; Kuznetsov, 2000).

Novaya Zemlya Island, the extension of the Ural fold belt, shows reef development in the early Emsian, then middle to late Eifelian through middle Givetian, with erosion at the end of the Givetian (Cherkesova, 1988; Zadoroshnaya et al., 1990a). In the Russian arctic, Taimyr and Severnaya Zemlya represent the northern flanks of the Siberian plate, while the New Siberian islands, e.g., Kotelnny, were part of the Kolyma plate. On the northeastern slopes of the Urals, Givetian patch reefs were accompanied by volcanics, indicating probable island fringing reef types (Antoshkina, 1998). Vaigach Island and Pai-Khoi peninsula of the polar Urals had extensive seaward- and eastward-prograding reef massif outcrops, with reefs to 80 m thick, in the Eifelian and Givetian. Similar reef complexes stretched southward almost the entire length of the eastern slopes of the northern Urals to northern Kazakhstan for over 2000 km (Zadoroshnaya et al., 1990a). On the tectonically active east



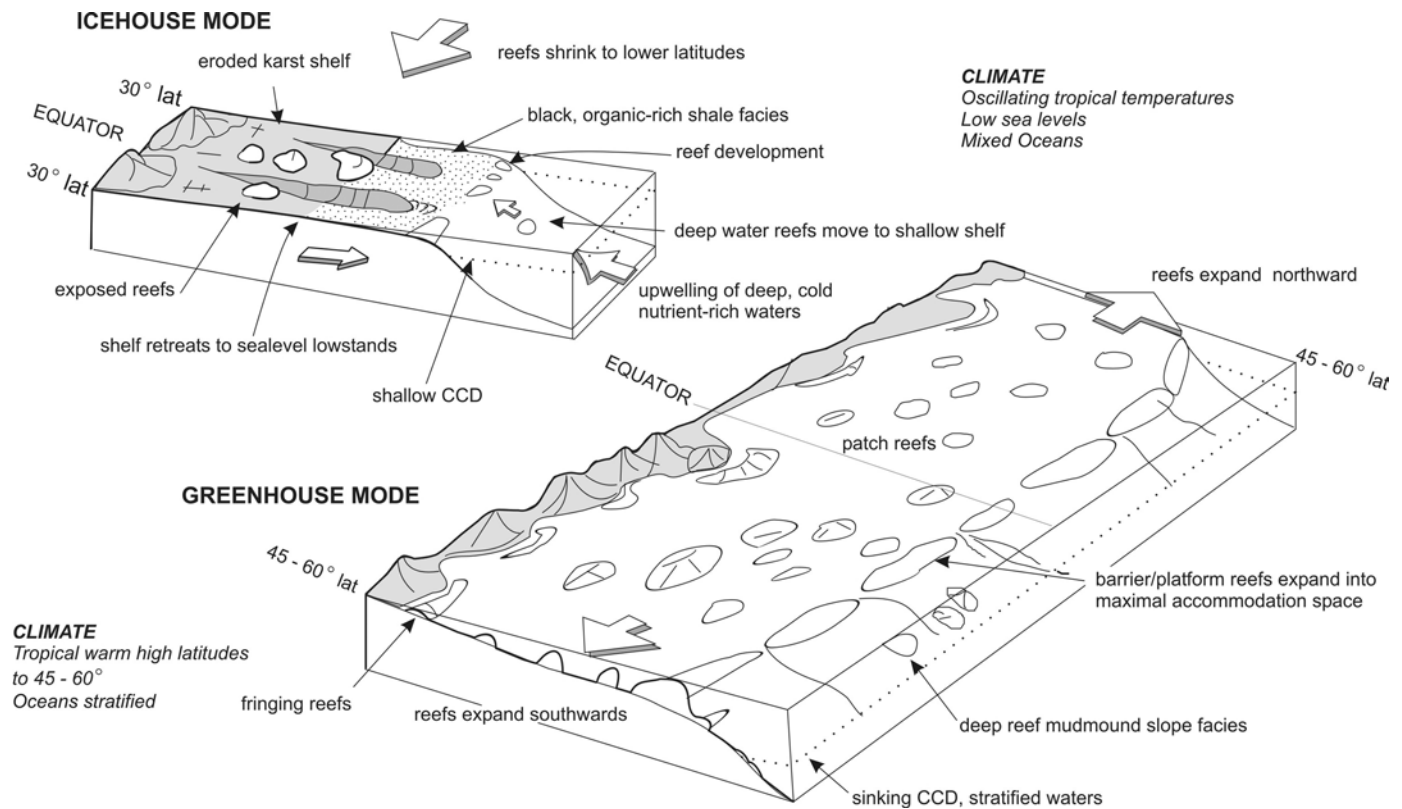


Figure 5. Schematic sketch of reefs in the Devonian calcite ocean system. During the Middle Devonian supergreenhouse (lower figure) with sealevel highstands, and stratified warm surface waters, reefs expanded into high latitudes ( $40^{\circ}$ – $60^{\circ}$ ) and occupied vast accommodation space on flooded continental interiors, as well as wide platforms. During the Late Devonian (Famennian: upper figure) sealevel lowstands and regressions favored higher Carbonate Compensation Depths (CCDs), and more vigorous oceanic advection, as icehouse episodes shrank reefs to lower, equatorial latitudes (corresponding to Holocene interglacial norms).

flanks of the south Urals, large and thick reef complexes were also developed from the Emsian-Eifelian through late Givetian, associated with andesitic-basaltic tuffs, followed by an erosional hiatus and further Frasnian reef growth (Stepanova et al., 1985). Zadoroshnaya et al. (1990b) noted the establishment of Famennian microbial (“algal”) fringing reefs and atolls on the mobile, volcanic eastern island arc belts, showing that such reef complexes were maintained as carbonate platforms from the Middle Devonian metazoan-dominated suites.

### South European Microplates (The South European Archipelago, or SEA)

Flanking the north edge of Gondwana proximal to northeast Africa were a suite of micro-island plates up to 500,000 km<sup>2</sup> in area, e.g., (1) Spain, (2) Sardinia, (3) possibly parts of Armorica, and extension to the Prague Basin, (4) the Montagne Noire, and (5), the Carnic Alps to Croatia. Here, these are labeled the South European Archipelago (Fig. 1). Whether these were fused into a single plate that subsequently separated into smaller units or were always separate plates forming an archipelago is unclear. Vai

(1991) suggested that most of these microplates were contiguous to North Africa and that the Carnic Alps were perhaps located on the south flank of neighboring Kazakhstan. Another aspect not generally agreed upon is how close these plates were to the north margins of Gondwana in the Devonian, or whether some plates were indeed part of Laurussia, the “Old Red Continent.” Franke (1999), in contrast, took the view that the Rhenohercynian belt was a passive plate margin extending from the Avalonia microplate and fused to Laurussia, and that Armorica was incorporated therewith, as well as the Bohemian massif, the Prague Basin, and the Sudetes. Hladil et al. (1999) also placed Moravia and the Prague Basin adjacent to the Old Red Continent to the north. In this paper, the South European Archipelago is shown as an archipelago along the northern margin of Gondwana, as indeed there appear to be closer faunal similarities between the Massif Armoricaïn, Montagne Noire, Prague Basin, and the Carnic Alps, and distinctions from the Old Red faunas. If these microplates are considered as a discontinuously distributed, “Bohemian facies” reef tract from Spain through the Montagne Noire and Prague Basin (Golonka et al., 1994), it would have been ~1600 km in length.

However, Hladil et al. (1999) also indicated in their palinostatic reconstruction that the Moravian karst area was part of a large, tectonically dismembered, Rhenish-type (or Bohemian-type) basin along the southern margin of Laurussia from the Emsian through Carboniferous. Considered as a unit, or as proximal units, these plates roughly straddled 30° latitude in a position due north of the Sahara, i.e., between Morocco and Libya. Baltica had already collided with the eastern margins of Laurentia in the Late Silurian or Early Devonian, closing the Rheic Ocean to form a single, large “Old Red Continent,” also known as “Laurussia.” There was progressive closure of the Rheic Ocean that separated Laurussia from the South European Archipelago from the Emsian through Givetian. Initially, this oceanic separation was on the order of 1500 km, but by the end of the Givetian, some millions of years later, the Rheic Ocean had shrunk to a sea lane <300–500 km wide (Fig. 4). This must have deflected warm currents back into a large ocean surrounded by the horseshoe made by Laurussia and central to eastern Gondwana, perhaps stimulating the dramatic losses in the late Givetian, Old World benthic coral, stromatoporoid and brachiopod faunas.

During the Emsian, reefs and coral biostromes were patchily, but vigorously developed along relatively short platforms and margins of northern Spain (Cantabria), and the westerly Pyrenees (Fernandez-Martinez et al., 1994). Carbonates flanked the northern side of the Spanish plate, from the Oviedo area to the Mediterranean Pyrenees, for ~800 km. Massive, possibly reefal carbonate facies of Emsian age occur in the Basque Pyrenees and in the subsurface, according to Blicek et al. (1988). Though reefs were apparently missing in the Eifelian of Spain, they were present in the central Pyrenees, and the whole region was reefal in the Givetian, from east to west. In the Montagne Noire of France, deepwater, aphotic, nonrigid sponge mudmounds with abundant stromatactis structures, in slope facies, were the main late Emsian reef development (Bourrouilh and Bourque, 1995; Bourrouilh et al., 1997; Flajs et al., 1996a), though they disappeared thereafter in the Devonian.

In Sardinia, the more than 60-m-thick mudmounds in the Pragian Mason Porcus Formation contain tabulate and colonial rugose corals (Gnoli et al., 1981, 1988, 1990). Emsian-age reefs with Uralian affinities, especially the *Karpinskia* giant brachiopod fauna, were present in western Slovenia (Krstic et al., 1988) and the Carnic Alps (Vai, 1998). Vai (1991) reconstructed a deep-water Bohemian facies and shallow water, isolated, Bahama-type platforms with reefs in Uralian facies for the Devonian. Reefs appeared here in the Lochkovian; larger reefs up to 350-m-thick identify the Pragian and extended maximally during the Eifelian, culminating in the Givetian. Vai (1998) placed the Carnic Alps–Slovenia platform as an extension of the Uralian platform on the east margin of the Russian Platform, a position fully justified on the basis of faunal similarities of the reefs. During the Frasnian, smaller Carnic reefs were present, and Late Devonian extensional tectonics made these platforms founder and drown (Vai, 1998). An alternative explanation might be that due to the closure of the gap between Gondwana and Laurussia, and the

separation of the Rheic from the Uralian Ocean, as shown by Vai (1998), reefs were eliminated via cold waters upwelling from the southeast, as warm waters were diverted on the Uralian side. This concept is supported by increased radiolarites spreading into shallow waters in the latest Devonian and Carboniferous (Vai, 1998). From the Frasnian to Famennian, carbonate production on the Carnic platforms dropped from 150 m to <25 m thickness, a loss of more than 90% (Ferrari and Vai, 1966). On the Austrian side of the Carnic Alps, Schönlaub (1998) suggested a depocenter for reefs in the Kellerwand and Hohe Warte area, which produced 1100 m of shallow water carbonates with patch reefs in the Lochkovian through Pragian, and a massive platform reef peak in the Givetian–Frasnian.

In the Prague Basin, there were both mudmounds and small coral-stromatoporoid patch reefs (the Koneprusy reefal limestone of mostly Pragian age; Chlupac, 1988), but the Prague area was already 10° closer to the equator than the Carnic Alps. Emsian through early Eifelian mudmounds and bedded limestones with stromatactis fabrics in the Koneprusy area were described by Flajs et al. (1996b); this facies persisted for several million years. On the Bohemian Massif, Moravian reef buildups covered roughly 6670 km<sup>2</sup> during the Eifelian and Givetian, continuing into the Frasnian (Hladil, 1986, 1988). Reef growth appears to have been temporarily disrupted during the late Givetian during one of several megacycles (Hladil, 1994). Reef decline began in the late Frasnian, and reefs disappeared by the Famennian. Hladil et al. (1999) identified considerable collision activity and crustal shortening in the Emsian of the Saxo-Thüringen through Moravian areas, some of which were detrimental to reef growth. In the former Yugoslavia, massive reef limestones are known from Emsian and Middle Devonian rocks astride the Bosnian sill in the Dinaric Alps (Vranica Mountain: Krstic et al., 1988). Some of these are preserved as slumped reef breccia carrying a Uralian fauna.

#### Northwestern Gondwana (Saharan Reef Tract)

The largest continent of the Middle Paleozoic was Gondwana, consisting of Africa, South America, Arabia, India, Antarctica, and Australia (Figs. 1, 3–4). Most of the marine shelves of Gondwana, as it centered around the south pole, represented cold climate shelf areas, replete with siliciclastic sediments and a Malvinokaffric, cold to cool temperate invertebrate fauna. Carbonate platforms and reefs were absent except on the northern fringes reaching the 45° to 30°S latitudes around the belt from Mauritania–Morocco into Algeria. Reefs are still unknown to the east in Tunisia and Libya. The reefs of the western “Spanish” Sahara near Zemmour (Saharawi People’s Republic) mark the southern end, and reefs extended, probably discontinuously, to Morocco and Algeria for some 1200 km. The northern shelf to ramp tract was up to 200 km wide along the north margin of Gondwana at the limits of coral reef growth in late Emsian time. It appears to have consisted of an inner shelf, separated from an outer shelf by a land area assigned to the western Meseta (Gendrot

et al., 1969; Gendrot, 1973; Benbouziane et al. 1993). El Hassani and El Kamel (2000) suggest the primary controls of patch reef, atoll, and barrier reef development in the Moroccan Meseta were tectonic highs. Elloy (1973), Benbouziane et al. (1993), Cattaneo et al. (1993), Hilali et al. (1998), and El Hassani and El Kamel (2000) noted the growth of shallow water coral-stromatoporoid reefs on the Moroccan shelf Meseta continued from the late Emsian, and may have reached a peak during the Givetian. The area was emergent by the middle Frasnian.

The relatively thinly developed, shallow water carbonates and small patch reefs of the Meseta and Maider Basin differ from deeper water Kess-Kess mudmounds in the Emsian of the Tafilalt area to the southeast, with flank deposits rich in nautiloids and ammonoids. Montenat et al. (1996) proposed that the Kess Kess mounds may have been tectonically controlled, but others suggest these were the result of microbial activity around submarine hydrothermal vents (Belka, 1998), and thus their development was unrelated to that of normal shelf reefs or slope mudmounds affected by climatic events. Moroccan (Anti-Atlas and Meseta) and West Saharan reefs of Emsian age gave way to relatively small tracts of coral-stromatoporoid patch reefs, shelf atolls, and small barrier banks in the Eifelian and early Givetian. This suggests relatively warm surface waters in the Middle Devonian, despite high latitudes (Figs. 3–4). However, reefs completely disappeared in northwestern Gondwana during the Frasnian and Famennian. Pedder (1999) indicated that the geographic affinities of the early Givetian rugose coral fauna of Morocco, at a time when reefs still occurred in the Maider Basin, were with faunas from Spain, the Pyrenees, and Moravia, situated on island plates to the north, and that no more than 17% of the Moroccan fauna had taxa in common with eastern Laurentia (i.e., the Appalachians).

#### **North Central Gondwana (Near East: Iran, Afghanistan, Pakistan)**

On the north-central flanks of Gondwana, sponge-coral reefs appear to have been absent. In the Arabian peninsula, part of the African-Arabian plate, small microbial (“stromatolitic”) mudmounds of late Emsian age, up to 10 m in diameter and <5 m high occur; these are associated with bryozoans and rare solitary rugosans (Al-Laboun and Walthall, 1988), representing a relatively cool water, or stressed, reef spectrum. The Arabian microbial reefs were located at about the same high latitude of 45°S as the Saharan reef belt (above); no other reefs are reported to date from this area. To the north of this region, in Turkey and the Caucasus (Georgia, Armenia), reefs appear to have been undeveloped in the Emsian mixed siliciclastic-carbonate facies through the Middle Devonian, though coral and stromatoporoid faunas are known (Mamedov and Rzhonsnitskaya, 1985). These areas were possibly an extension of the Mediterranean terrane blocks flanking the northern margins of Gondwana.

To the north of the Gondwana supercontinent, adjacent small plates of central Asia, such as those from southern Afghanistan

and Pakistan, were episodically marked by well developed reefs during the late Early and Middle Devonian (Stauffer, 1968; Gaetani, 1968). For example, Emsian reef limestone was present along a volcanic belt in central Afghanistan, according to Wolfart and Wittekindt (1980). This reef belt was said to extend into northern Pakistan. Mistiaen (1995) noted that in Afghanistan, small, <10-m-high stromatoporoid, tabulate coral, microbial reefs also began in the Emsian, corroborating that reefs there in the 30°S latitude were developed on a series of microplates, or a large, elongated plate situated close to the northern flanks of Gondwana. Whether Emsian reefs were present in the neighboring areas of Iran (Gaetani, 1968; Dastanpour, 1996) and Pakistan (Stauffer, 1968), dominated by siliciclastics and evaporites at this time, is unclear, though the regions have a similar geologic history. Assuming Middle Devonian reefs were developed from central Iran through southern Afghanistan and into neighboring Pakistan, this would have been a tract ~1800 km long (Table 1). There are extensive hiatuses in the Early Devonian and Eifelian of Iran (Dastanpour, 1996) and Afghanistan. Brookfield and Gupta (1988) reviewed the Devonian of the Pakistan through Himalayan regions, though reefs were unidentified, and the dating of many units remains in question. During the late Middle Devonian and Frasnian, reefal carbonates were expanded into eastern Iran and Pakistan (Wolfart and Wittekindt, 1980). Jux (1969) and Mistiaen (1985) have also indicated that reef growth continued in this region during the Frasnian.

#### **Tian Shan Fold Belt (Uzbekistan, Tadjikistan, Kirgizstan, Northern Afghanistan)**

The Tian Shan Fold Belt (Russia), including areas of Uzbekistan, northern Afghanistan, and Tadjikistan, contains widespread Emsian through Middle Devonian reefs, as well as some Frasnian reef complexes (Zadoroshnaya et al., 1990b; Dronov and Natalin, 1990). These areas appear to represent smaller, mobile “island continent” terranes, proximal to the northeastern and central margins of Gondwana. In southern Uzbekistan, thick coral-stromatoporoid-calcimicrobial reef platform facies, with back reef lagoons, appear to be more prominent in the Middle Devonian Khodzhakurgan Formation than in Early Devonian strata dominated by volcanics and siliciclastics (Kim et al., 1984). In southern Fergana (Tadjikistan), the upper part of the atoll-like Kiziltash reefal mudmound, 5 km long and ~500 m thick, is of Eifelian age (Dronov, 1993). To the southeast of Tadjikistan, in the central Pamir Mountain ranges, reefs of Emsian through Givetian age were also developed on a miogeosynclinal platform up to 1.5 km thick (Ioganson, 1990b). The tectonic relationship of the Pamir Reef belt to the Tarim-Karakorum plate is disputed (see below). The Uzbekistan-Pamirs reef tract, starting at the Nuratau ranges in the west, shares much in common with Middle Devonian reefs of central Tadjikistan and the Tadjik Pamirs, and northern Afghanistan. This Pamirs tract was just less than 1000 km long, if it ended in the Pamir ranges, and longer if it joined the Chinese areas along the borders (see Karakorum plate below).

## Kazakhstan

Kuznetsov (2000) outlined a Lower and Middle Devonian reef belt ~1000 km long along the eastern, tectonically active side of Kazakhstan, influenced by calc-alkaline volcanism. Uplifted land areas were located to the west. Lochkovian reefs, located in the 8–15° latitudes north (Zonenshain et al., 1990a) are kilometers in diameter and up to 120 m thick: they do not appear to have been continued into the Emsian and Eifelian, however, though they reappeared in the Givetian. A similar outcrop belt is located in the Tarbagatai Mountains of western Junggar in Xinjiang, China, with Kazakhstan faunal affinities. In the northern and central Kazakhstan Dzungar area, reefs were renewed in a Givetian carbonate pile up to 2 km thick, but reefs were missing in the Frasnian (Zadoroshnaya and Nikitin, 1990). Famennian through Tournaisian calcimicrobial “Tubiphytes” patch reefs, atolls, and mudmounds were developed on a carbonate platform up to 150 km wide and 1000 km long on the northwestern side of Kazakhstan (Karatau ranges), but not the eastern flanks (Pavlov et al., 1988; Cook et al., 1994). In the “Junggar” region of northwestern Xinjiang in China, a rich early (Emsian) and Middle Devonian coral fauna indicates affinities with Kazakhstan (Deng, 1999), but reefs are undescribed thus far. If Middle Devonian reefs were developed from the eastern side (Kenzhebasai River, west of Balkhash Lake) of the extensive carbonate platform in Kazakhstan to proximal Xinjiang province of China, this tract would be ~1600 km long.

## Karakorum-Tarim Plate

Today this plate extends from the Tarim Basin in western China through the Karakorum ranges of North Pakistan (and possibly the Pamir ranges of Tadjikistan). An ophiolite belt separates the Tarim Block from the Kazakhstan and Dzungar plates today, indicating the probable initial separation and subsequent collision of these plates took place after the Devonian. It has been suggested that the Karakorum Block and Tarim Block may have been separated (Talent et al., 1986); here it is taken as a single unit, following current Russian usage (Belenitskaya and Zadoroshnaya, 1990). What its relationship is between the Tien Shan ranges of Tadjikistan and the neighboring areas of China is unclear. The southern Pamir fold belt contains both stable miogeoclinal carbonate platform and unstable margins with allochthonous debris flows. Rugose, tabulate coral and stromatoporoid reefs indicate normal tropical carbonate shelf conditions, with the sequence up to 1.5 km thick on the Russian side (Ioganson, 1990b). The southern Chinese Tian Shan Range is shown as an accretionary collisional fold belt on the southern side of Kazakhstan by Yolkin et al. (2000). This suggests that the area may have been constructed of smaller plates accreted to Kazakhstan or the Dzungar at a later date. For the Karakorum-Tarim plate, Kuznetsov (2000) reconstructed a very elongate continent up to 5000 km long, with a ~1000-km-long reef belt mostly between the 5° and 10°N latitudes and in the northern Pamir to Tarim portions. Thus far, little

information on reefs is available from the Tarim Basin in China (Zhou and Chen, 1992; Liao et al., 1992) and the Tian Shan and Karakorum Ranges (Wen, 1998). Where the Tian Shan fold belt, presently located southeast of Kazakhstan and neighboring China, was situated in the Devonian seems unclear, or disputed. Sun and Chen (1998) cited Emsian reefal limestones from the Hongshandaban Formation of the Karakorum-Kunlun Mountains, and regarded their brachiopod faunas as similar the Old World faunas of the Urals and South China.

## Siberia

On the southwestern margins of Siberia (Salair, Kuznetsk, Minusinsk Basins), Paleozoic reefs reached their maximal development in the Devonian (Yolkin et al., 2000). There is some debate whether Siberia and Mongolia and the northeastern plates were close to each other, or distal, or where they were located latitudinally. In the Salair Range, coral-stromatoporoid reefs were present in the middle Lochkovian and Pragian, and discontinuously from the Emsian through Givetian, with a gap in the late Givetian and early Frasnian (Yolkin et al., 1997). These Emsian-Frasnian reefs were part of a major belt stretching north-south in west central Siberia, about 1500 km from the middle Enisei River to the Gornoi Altai (Ioganson, 1990c), with peak development in the Middle Devonian primarily in stable platform settings. Ivanova et al. (1964) plotted Eifelian coral-stromatoporoid reefs for the Minusinsk and Kuznetsk basins, but identified volcanism and regression in the Givetian. On the far western flanks of the Siberian platform, i.e., the eastern slopes of the Urals and the subsurface of the western Siberian lowlands, there was a tectonically active collisional zone in the Devonian (Belenitskaya and Zadoroshnaya, 1990). Fringing microbial reefs flanked areas with active flysch development in the Devonian, along the present day eastern slopes of the Urals (Chuvashov and Shuiskii, 1988). It is difficult to interpret such reefs as being either part of the Russian platform or western Siberia. In north central Siberia, the Taimyr peninsula, a platform carbonate with reefs was present in the Givetian, associated with back reef *Stringocephalus* (Cherkesova, 1988).

In southeast Siberia, close to the Amur River border (Amur-Okhotsk fold belt), massive microbial-coral and bryozoan reefs of Eifelian age range from 250 to 800 m thick and extend discontinuously for nearly 400 km (Belyaeva and Ioganson, 1990). These apparently reflect a passive margin and broad shelf setting. Whether these may be tectonically part of the Mongolia or North China plates or whether they pertain to the southeastern margin of Siberia is uncertain. Another remote Middle Devonian reef area several hundred kilometers long is indicated in the Khabarovsk region (Kuznetsov, 2000).

## Verkhoyan-Kolyma Plate (Northeast Russia)

Devonian reefs were well developed along the western sides of the Kolyma block of northeastern Russia. Lower Devonian reefs of the Tas-Khayakhtakh Mountains are exposed in a belt

about 3–10 km wide and 150 km long, with reefs to 200 m thick, and from 0.5 to 3 km long (Ioganson and Baganov, 1990). Reef frame-builders were calcimicrobes, algae, and tabulate corals, with growth ranging from the middle Lochkovian, peaking in the Pragian and ranging to the Emsian. A break in the Eifelian, with more siliciclastic input followed by a disconformity, saw renewed vigorous algal-tabulate-amphiporid reef growth in the Givetian with reefs extending ~100 km in length and up to 500 m thick into the Frasnian (Vishnetskii and Baganov, 1986). These Lochkovian-Pragian reef belts were further spread ~200 km into the upper Selenyakh River reaches to the north. Givetian and Frasnian reefs were also present northwest of the Kolyma River, in a sequence up to 500 m thick on the stable platform of the Ulakhan-Tasskoi area (Ioganson and Bazanov, 1990). In the southwestern Kolyma River zone, the Alazei foldbelt, decameter-thick “biohermal massifs” are dominated by corals, stromatoporoids, and algae of Early Devonian age associated with dolomites and evaporites up to 1 km thick (Ioganson, 1990a). Dolomitized reef complexes are also present in rocks of Givetian and Frasnian age, but not as thick as those preceding. If these Kolyma Reef belts are part of a large platform, this may have stretched more than 800 km. Devonian reefs appear to be generally absent, however, in the Chukot block to the northeast, though they are present in the Middle Silurian and Early Carboniferous. An exception may be along the Omolon River zone, where an active margin with siliciclastics, andesites, and tuffs featured 40-m-thick patch reefs with algae, corals, and stromatoporoids of Middle Devonian age, but no Early or Late Devonian reefs (Ioganson, 1990a). The northern margin of the Kolyma plate featured the development of early Eifelian reefs on offshore Kotelny Island in the Arctic Ocean (New Siberian Islands; Cherkasova, 1988). How much their faunas match those of the Canadian Arctic Blue Fiord reef faunas is not yet clear, but both areas lack Frasnian carbonates, except for Banks Island.

### **Mongolia (Tuva Plate)**

Various reconstructions have placed Mongolia, parts of the Russian Altai, and Inner Mongolia (the Tuva plate) in high north latitudes of 45–60° during the Devonian, as a lateral extension of an inverted Siberian plate (Golonka et al., 1994). Yolkin et al. (2000) interpreted the Siberian Devonian continent as including Mongolia, basically sutured in the alignment they possess today. Kuznetsov (2000) showed the Altai and Salair as two separate plates in the vicinity of Mongolia. He also marked central Mongolia, with Devonian reefs, as an isolated, elliptical small continent about 1500–2000 km long, roughly halfway between north China and Kazakhstan, in the lower 20–30°N latitudes. Rong et al. (1995) argued for alignment of the Late Silurian Mongol-Okhotsk faunal province as fixed to the eastern side of Siberia, i.e., no separate plate for Mongolia. Unique *Tuvaella* brachiopod and endemic Tuva-Mongolian coral faunas mark a high degree of provinciality in the Late Silurian and Early Devonian, and these argue for separation of both parts of

Mongolia from Siberia. Thus, two interpretations exist, one uniting Tuva and Siberia during the Devonian, and the other creating an isolated paleocontinent for the Tuva-Okhotsk-Mongol region, separate from Siberia and possibly extending to the Hingangling Ranges of northeastern China.

The development in Mongolia of extensive carbonate platforms, and commonly reefs, took place from the Late Ordovician (Caradoc) through Middle Devonian, ceasing in the late Givetian (Minjin et al., 2001). Sharkova (1986) plotted an 1800-km-long, ~150-km-wide reef platform, flanking the southern side of present Mongolia. Tabulate-rugose coral reefs are developed in the Orgol Formation (Lochkovian) and upper Dungee Formation (Emsian) in Mongolia (Suetenko et al., 1977). In the Shine Jinst area of south-central Mongolia, the early Emsian Hurenboom tabulate and rugose coral “reef,” or carbonate bank, is locally developed in the Chuluun Formation, extending into the Eifelian (Sharkova, 1980, 1986; Minjin, 2001). Facies indicate an active tectonic margin interrupted by volcanics to the south and a stable continent to the north (Minjin et al., 2001). Although carbonate deposition continued, reefs ceased by the Givetian, and thinly bedded black limestones and shales took over in the Famennian and Tournaisian (Alekseeva, 1993).

### **North China Plate**

The tectonically active north margin of the North China plate saw reef development in the Emsian, Eifelian, and early Givetian in Inner Mongolia and Heilongjiang provinces. Such reefs were associated with strong siliciclastic pulses and volcanism. Tabulate-rugose coral patch reefs of Emsian age belonging to the Unur Formation occur in the Hingang Mountains (Su, 1988). The Dean Formation of Eifelian age contains coral reef limestones rich in brachiopods, and the Hoboshan Formation (early Givetian) contains microbial (“algal”) reefs associated with acid volcanics (Su, 1988). Frasnian reefs are absent. In the Famennian, siliciclastics and terrestrial settings took over. This suggests a decline in reef growth from the early Givetian onward. The complete extent of the reef belt is unknown at present, but it was ~700 km long. A relationship to the Amur-Okhotsk area of Russia is possible, though not verified. North China is plotted in very high latitudes between 30° and 60°N during the Middle Devonian by Kuznetsov (2000), in low latitudes straddling the equator by Golonka et al. (1994), and adjacent to Australian Gondwana by Talent et al. (2000). The affinities of the North China plate with Mongolia-Tuva are unclear, but today the two areas are separated by an ophiolite belt. Talent et al. (2000) placed the North China plate against the north shelf margin of Australia from the Early to Late Devonian, with the South China plate to the west, both straddling the equator.

### **South China Plate**

South China was a separate plate south of the equator during the Devonian, probably separated from northwest Australia by a

relatively narrow ocean (Talent et al., 2000). The area encompasses a stable platform carbonate belt reaching eastward from Laos, Cambodia, and Vietnam, past Burma, to Yunnan, Guangxi, Guizhou, and Hunan provinces in southern China, for a passive margin more than 1700 km long (Zeng et al., 1992). A collisional, active margin with reefs has not been identified; land areas were on the northern margins of present day South China. How much of the South China plate had reef growth remains uncertain, but coral-stromatoporoid reefs appear centered in the area from Yunnan east via Guangxi, Guizhou, and Hunan provinces, for ~1000 km. Maximal area for carbonate platform development was during the Emsian, Eifelian, and Givetian (Bai et al., 1994; Yu and Shen, 1998; Shen et al., 1994). For much of the earlier Devonian, the continent was emergent, with reefs commencing in the late Pragian as small patch reefs and expanding to larger tracts during the Emsian (Yu and Wu, 1988). In the Nandan Basin of southern Guangxi province, the 830-m-thick Dachang Reef began its growth just above the top of the Emsian *perbonus* zone and continued into the late Eifelian *ensensis* Zone for a duration of ~15 m.y. (Bai et al., 1994).

Maximal reef growth in the southeastern portion of the South China plate was during the middle Givetian, especially in the *varcus* and *herrmani-cristatus* zones of the reefal Tangjiawan Formation, with a lowstand in or at the top of the *disparilis* zone (Shen et al., 1994; Wu and Shen, 1998). In South China, the Givetian-Frasnian boundary is still debated to lie either below or on top of the middle *falsiovalis* or *pristina* zone. There are multiple “nickel events,” used in China to define “anoxic” episodes in the *hermanni* through *disparilis* zones, below the Givetian-Frasnian boundary, with a regressive spike in the upper *disparilis* zone, but there was no marked latest Givetian regression or reef proxy signal (Bai et al., 1994). The large Middle Devonian carbonate platform was broken up by late Givetian *varcus* time into smaller, isolated Bahama-type platforms with reefs separated by basinal Nandan-type black shales during the Late Devonian, and metazoans were replaced by calcimicrobes in Famennian reefs (Yu and Shen, 1998).

### Australia-Papua New Guinea Plate

Emsian and Eifelian reefs of Australia were primarily confined to the tectonically active, unstable eastern margins of Australia, associated with volcanics and siliciclastics (Crook, 1961; Wolf, 1965). Thus, there was not an apparently large scale, continuous barrier-rimmed platform on which reefs could have been developed, as there was in western Canada, but probably a number of smaller, isolated basins (Talent et al., 1986). Many reef bodies are found as allochthonous tectonic debris flows, presumably as collapsed margins or as slumps along the eastern Australia margins for a distance of more than 2000 km, effectively representing “lost” carbonate platforms as they are only partly preserved today (Talent and Mawson, 1999; Talent et al., 2001). The Nubigrin calcimicrobial reef blocks, occurring as allochthonous units, are of late Lochkovian through Emsian age (Wolf,

1965; Conaghan et al., 1976). Pohler and Kim (2001) outlined rugose coral framework and “organic buildup facies” in the Emsian of New South Wales. These extended as Eifel-Givetian stromatoporoid reefs close to 20 m thick within the Moore Creek Formation of New South Wales (Pohler, 1998), part of a volcanic island arc complex. In Queensland, Jell and Zhen (1994) cited small coral-stromatoporoid patch reefs, mostly of Givetian age, from the Fanning River Group. No outcrop or drillcore data is available on the extension of the east Australian active margin, e.g. the presence of reefs in Papua New Guinea and West Irian, a tectonically complex area primarily covered by tropical rainforest today but ideally located for reefs in the Devonian paleotropical equatorial belt on the northern tip of the Australian plate (Talent et al., 2000).

On the passive western margin of Australia, Middle Devonian reefs appear to have been scarcer, except for the commencement of reefal carbonates in the middle to late Givetian of the Canning Basin (Read, 1973a, 1973b; Grey, 1991; Southgate et al., 1993). These continued into the more spectacular, exposed, ~400-km-long reef platform during the early and middle Frasnian (Playford and Cockbain, 1989; George and Powell, 1997; George and Chow, 1999), with prominent shallow water stromatoporoids, corals, and shallow as well as deeper calcimicrobes within the photic zone (Paul, 1996). In the subsurface, subaerial karst has been difficult to find in the Canning Basin, and no events are specifically known yet to characterize the end Givetian regressions found elsewhere, as the Pillara Formation apparently spans the Givetian-Frasnian boundary without a break (Read, 1973a; Brownlaw et al., 1996). Emsian to Givetian reefs appear to have been absent in the Carnarvon Basin to the far west.

### HOW WERE DEVONIAN MEGAREEFS PRODUCED?

Questions emerge from this global reef snapshot of the Middle Devonian. With examples from the Middle Paleozoic maximum, it is evident that megareef belts were produced in calcite oceans under global supergreenhouse climates featuring high tropical sea surface temperatures. Several factors came to play:

1. Warm sea surface temperatures stretched reefs to very high latitudes of 40–50° (or possibly higher if some reconstructions based on paleomagnetic data are correct), and may be used to constrain paleolatitudinal positions of major plates. High latitude reefs had one drawback in that, at their outer limits, there was reduced solar input during the winter months because of fewer daylight hours, though this may have been balanced by longer summer hours and rapid growth. The Middle Devonian supergreenhouse may have had parallels in the Cretaceous greenhouse model of Poulsen et al. (1999) and Johnson (1999), for which equatorward shifts of atmospheric circulation, polar warming, and high latitude increases in precipitation, climate reorganization of atmospheric low and high pressure regimes in the tropics, and a low pole-equator temperature gradient were proposed.

2. To create such megareefs required sea-level highstand systems tracts flooding wide areas of low elevation continents; i.e.,

they inhabited vast epicontinental seas, unlike limited Holocene open shelf systems (e.g., Givetian, Fig. 4).

3. Megareefs were favored on wide, open passive margins, with good open ocean access, inducing free mixing and normal salinities (Figs. 4 and 5).

4. Large Paleozoic reefs required the evolution of large, reef-building, modular, photozoans (i.e., skeleton builders utilizing photosynthetic symbionts) with rapid composite growth rates, e.g., giant colonial corals such as tabulates and rugosans, and calcareous stromatoporoid sponges, and also a wide selection of encrusting, frame-fixing calcimicrobes (for contrasting view, see Hallock, 1996). Devonian megareefs were exploited by warm temperature-adapted, rugose and tabulate coral framebuilders with calcite skeletons, but the reef niche was also occupied by nonspiculate stromatoporoid sponges with a basal aragonitic, or possibly high Mg-calcite skeleton exposed to light (probably also photozoans). Red and green calcareous algae generally played only a small role in Devonian metazoan reef building.

5. The giant and complex colonial forms of corals had tropical growth rates (40–100 mm/yr; Gao and Copper, 1997) comparable to those of modern scleractinians. This suggests that these forms were zooxanthellate, and that such symbioses assisted in achieving accelerated reef growth. Massive, multi-meter thick and wide stromatoporoid sponges had relatively slower growth rates (1–10 mm/yr), and it is unclear if such forms had dinoflagellate symbionts; i.e., were they photozoans? However, much higher CO<sub>2</sub> saturation states in shallow shelf areas during the Middle Paleozoic suggest that zooxanthellae probably were obligate symbionts and providers of O<sub>2</sub> for calcification, to maintain even modest growth in aragonitic sponges. There is, as yet, no evidence that growth banding was more prominent in high, temperate latitude reef organisms in the Devonian.

#### WHY DID REEFS CONTRACT WITH CLIMATE CHANGE?

The issue of climate and reef distribution in the distant past is still speculative. Kiessling (2001, p. 754) suggested that “many of the changes [in reefs] are linked to changing nutrient requirements of the prevailing reef builders and nutrient availability in the oceans...ultimately controlled by climate change,” following the theme suggested by Wood (1993, 1999). It is difficult to find any direct proof of the relationship of Paleozoic reefs to nutrients or organic-rich sediments. Climate cooling during the Late Devonian (Frasnian/Famennian) mass extinctions was marked by an increase in phosphorites, and silica (radiolarite) deposition (Racki, 1999), and the concomitant loss of metazoan coral-stromatoporoid sponge reefs. It seems more logical that cooling reduced carbonate deposition rates by accelerating the death of tropically adapted, zooxanthellate reef builders (photozoans), and that the loss of metazoan reefs was not directly connected to nutrient increase. Joachimski and Buggisch (1996) confirmed positive  $\delta^{13}\text{C}$  values shifting about +2‰ above background norms for the two late Frasnian Kellwasser organic-rich carbonates in the late

*rhénana* and *linguiformis* conodont zones, just below the F/F boundary. They interpreted this rise as marking global flooding surfaces with relatively short-lived sea-level highs (accompanied by carbon deposition from deep, anoxic bottom waters dumped onto the shallow shelf), as mechanisms inducing cooling, i.e., that anoxia triggered cooling (sometimes called the “preservation model”). A counter explanation might be that cooling and vigorous watermass overturn triggered upwelling of nutrient-rich bottom waters, stimulating high surface plankton productivity, as well as growth of benthic algal turf on the reefs, and that high rates of carbon burial under shallowing and regressive shelf conditions produced the black shales (as suggested in modern “production models” by Pedersen and Calvert, 1990). This scenario would fit the widespread Devonian deposition of black shales under regressive coastal conditions, as seen in many late Frasnian and Famennian boundary sections (Copper, 2002). In contrast, Murphy et al. (2000) suggested a “seasonal mixing-efficient cycling” model (decoupled from water depth and temperature), to account for black shales in the Devonian Appalachian Basin.

Reef boundary conditions in the Middle Paleozoic were set largely by climatic cooling events, with the 90 m.y. long reef megacycle starting in the Silurian and terminating in the Devonian (Fig. 6). The Middle Paleozoic cycle commenced in the Early Silurian, 3–4 m.y. after the Ordovician-Silurian boundary triple glaciation, though the Silurian biota had already been initiated in the latest Ordovician stage (Hirnantian: Copper, 2001). Regressions in the Late Silurian (Pridolian) continued in the Early Devonian (Lochkovian-Pragian), when reefs retreated equatorward, became smaller in size, and endemic reef provinces were established. No glaciations are known from this time. Renewed glaciation during the Late Devonian (Famennian: Isaacson et al., 1999) marked major cooling episodes that eliminated most of the coral and stromatoporoid reef-building taxa and the metazoan reef ecosystem. Over the 21 m.y. long Famennian “recovery” period, patch reefs were populated by calcimicrobes, rare stromatoporoids, and lithistid sponges, and reefs were small-sized, or mud-mound-type structures in both shallow water and slope settings (Webb, 2001; Copper, 2002). At this time of climatic perturbation, the oceans moved to oscillating icehouse modes, the carbonate compensation depth (CCD) rose into shallower waters, as it does in cold oceans today, and oceans probably shifted largely to an aragonite mode of skeleton production (Sandberg, 1983; Webb and Sorauf, 2002), that reduced the importance of the remaining tabulate and rugose corals. Famennian surviving tabulate and rugose corals probably derived from relict refugial, deep-sea forms, persisted in the Tournaisian, but they rarely built significant reefs in such later Paleozoic shelf settings.

During the Late Paleozoic, boundary conditions for reef growth were changed by alignment of tectonically amalgamated plates that fused and shaped the supercontinent of Pangea. This horseshoe-shaped Pangea, opened eastward, blocked equatorial currents in low latitudes, producing a very warm Tethys, but creating large, cool shelf areas on the western sides of continents. Secondly, repeated glaciation-induced sea-level drawdowns

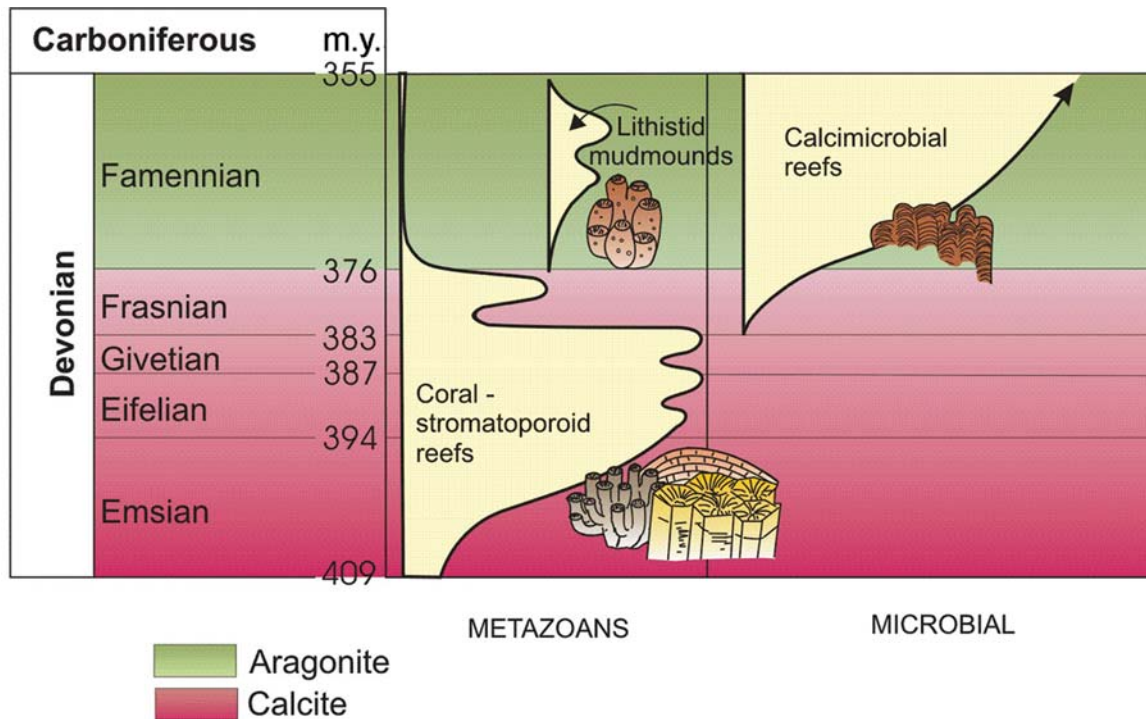


Figure 6. "Reef curve" during the Eifelian-Givetian, and reef crises during the Late Devonian as seen in expansion and subsequent loss of coral-stromatoporoid reef builders in the late Frasnian and rise of episodic development of regional mudmounds and calcimicrobial reefs in the 21 m.y. long Famennian. Full recovery of large-scale metazoan coral-sponge reefs never occurred in the switchover to aragonite oceans during the Famennian and Late Paleozoic, though small patch reefs of lithistid and stromatoporoid reefs were sporadic in the late Famennian (Strunian).

during regressive episodes eliminated reef and carbonate platform accommodation space, reduced the sizes of epicontinental seas, and shrank warm seas to lower paleolatitudes. This situation was comparable to that of the Pliocene-Pleistocene, with the closure of the Isthmus of Panama (Budd and Johnson, 1999). Thirdly, additional drawbacks in the Late Paleozoic were mountain-building cycles as a result of continental collisions: these triggered increased siliciclastic sedimentation and probably increased volcanism, drowning reef platforms in muds and silts, as in the Bay of Bengal and Kalimantan today. Fourthly, in the tropical belts, as warmer, more humid air was displaced northward into higher latitudes, heavy rainfall produced lower salinities in coastal shelf areas, probably favoring the establishment of large-scale Carboniferous Waulsortian mudmound growth, on which light- and temperature-independent heterozoan biota survived under cooler, stressed conditions (e.g., as for the Great Australian Bight today; James, 1997).

## CONCLUSIONS

The Devonian lasted some 63 m.y. (Okulitch, 1999), about the same duration as the Cenozoic, with the 26 m.y. long Emsian-Givetian episode representing the peak in Phanerozoic global carbonate production and widespread reef growth. Such coral-

stromatoporoid reefs expanded with high  $\text{RCO}_2$  levels and super-greenhouse climates and crashed as  $\text{O}_2$  levels rose (Berner, 1997). The following are some general observations:

1. During the Emsian-Givetian, reefs in low latitudes of  $<40^\circ$  were dominated by rugose and tabulate coral-stromatoporoid frameworks and keystone taxa, commonly with a significant calcimicrobial component acting as binders and encrusters in the reef core. The Givetian marks the peak of Devonian reef distribution and carbonate platform growth, following progressive expansion of metazoan reefs from the Emsian onward. The end Givetian marks a major collapse of reefs, exceeded only by the late Frasnian.

2. Reefs in higher latitudes ( $40\text{--}50^\circ$ ) were generally mudmounds of enigmatic origin, with a sparse metazoan cover (e.g., Kess-Kess mudmounds of Morocco and Algeria, mudmounds of the Montagne Noire, and Sardinia). Mudmounds less commonly featured prominent calcimicrobial biota such as *Girvanella*, *Rothpletzella*, and *Wetheredella*, suggesting that many grew in deeper waters or in shallow seas with high surface plankton production, diminishing light penetration. Reefs with coral-stromatoporoid frameworks were exceptional in higher latitudes.

3. As reefs declined, higher latitude reefs vanished first during the Late Devonian, e.g., on the northern margins of Gondwana (Morocco-Libya, Montagne Noire), though large reef tracts



in some lower paleolatitudes also vanished (e.g., Frasnian of the Canadian arctic).

4. Pre-Middle Devonian (Pridolian-Lochkovian-Pragian and early Emsian) reefs were patchily developed, probably largely as a result of relative sea-level lowstands, limited carbonate platform, and epicontinental reef accommodation space. Faunal provincialism was widespread.

5. Post Middle Devonian (Frasnian) metazoan reefs showed relatively lower, albeit cosmopolitan, biodiversity of corals, stromatoporoids, and accompanying shelly biotas, related to major losses of tropical reef-dwelling subfamilies and families toward the close of Givetian time. The Frasnian featured a restricted expansion of metazoan reefs worldwide, though metazoan reefs were prominent regionally in the Canning Basin of Australia, South China, the Urals, Banks Island, and Alberta.

6. The use of the reef database to reconfigure the latitudinal position of major tectonic plates seems feasible. Our reconstructions, for example, show that the Mongolia-Tuva plate may be located considerably further south than previously indicated (Golonka et al., 1994).

7. Care should be taken in drawing broad conclusions about reef latitudinal constraints when dealing with long periods of time, e.g., over millions of years. For example, within the 63 m.y. long Devonian, sharp variations in reef development are recorded, just as for the Cenozoic, covering roughly the same time span.

## ACKNOWLEDGMENTS

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