

# EARLY EVOLUTION OF THE PALEOZOIC STROMATOPOROIDEA

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## PROBLEMATIC EARLY CAMBRIAN RECORD

Examples of early Cambrian fossil groups have long been known to exhibit stromatoporoid-like skeletal features (see early summaries in WEBBY, 1979a, p. 112–115; 1986, p. 148–151). However, all now appear to have been produced by organisms that are unrelated to indubitable members of the Ordovician-Devonian Stromatoporoidea, as outlined below.

## ARCHAEOCYATHS WITH STROMATOROPOID-LIKE RESEMBLANCES

One small group of archaeocyaths belonging to the order Kazachstanicyathida KONYUSHKOV, 1967 (two suborders, two families, and three genera) developed comparable, well-integrated, modular, broadly thalamid (=sphinctozoan) to stromatoporoid-type structures [WOOD, ZHURAVLEV, & DEBRENNE, 1992; DEBRENNE & REITNER, 2001; and see *Korovinella sajanicum* (YAVORSKY, 1932) (Fig. 656, 1); and *Altaicyathus notabilis* VOLOGDIN, 1932 (Fig. 657)].

These forms generally bear closer organizational resemblances to mid-Permian–Holocene verticillitid (sphinctozoan) demosponge genera like *Stylothalamia*, *Menathalamia*, and *Vaceletia* (FINKS & RIGBY, 2004c, p. 712–719), only differing in tending to develop somewhat more fully integrated multioscular skeletal arrangements. In comparisons with typical Paleozoic stromatoporoids, the kazachstanicyathid genera *Korovinella* and *Altaicyathus* differ more fundamentally in developing perforate tabulae (equivalent to the cyst plates or laminae of stromatoporoids that are almost always nonporous), and the less fully integrated skeletal arrangements characteristically have lower skeletal densities

and smaller sizes. The Paleozoic stromatoporoids established biomineralizing habits some 60 myr later than the archaeocyaths and were an independent group of sponges with a nonporous, nonspiculate skeleton. The Kazachstanicyathida merely represent the end product of a divergent line of descent within the class Archaeocyatha. This apparent convergence possibly relates to adaptive pressures associated with reef building in warm seas that developed for a short time during the early Cambrian (Botomian). The small archaeocyath group has no ancestral relationships to later stromatoporoids (NESTOR, 1966b; WEBBY, 1986). There is no evidence that any of these forms, or any other member of the Archaeocyatha (cf. VLASOV, 1961), gave rise to the stromatoporoids.

## OTHER POSSIBLE CONVERGENCES

### Coralomorph Genus *Yaworipora* ZHURAVLEV, 1999b (Tabulaconida)

Two early Cambrian (Toyonian) so-called species from the Kuznetskii Alatau, Altai Saian Fold Belt of southwestern Siberia, were illustrated by KHALFINA (in KHALFINA & YAVORSKY, 1974, p. 39, 270–271, pl. 1, 1–2) without description (hence *nomina nuda*) and referred to the genus *Stromatocerium* (i.e., related to stromatoceric labechiids like those from the Ordovician). On this basis, KHALFINA and YAVORSKY (1967) argued that some Ordovician labechiid stromatoporoids were derived from stocks like the Cambrian species of so-called *Stromatocerium*. WEBBY (in STEARN & others, 1999, p. 18) tentatively associated KHALFINA's species in KHALFINA and YAVORSKY, 1974, with an unnamed stromatoceric genus (now described as *Vietnamostroma* NGUYEN, HUNG HUU, & MISTIAEN, 1998). However, ZHURAVLEV, DEBRENNE, and LAFUSTE (1993, p. 369)

had previously recognized the resemblance between KHALFINA's Cambrian species in KHALFINA and YAVORSKY, 1974, and the early Cambrian coralomorph *Flindersipora* LAFUSTE in LAFUSTE and others, 1991, and ZHURAVLEV (1999b) has since revised KHALFINA's species in KHALFINA and YAVORSKY, 1974, combining the two species as the new coralomorph taxon, *Yavoripora khalfinae*. This Cambrian coralomorph has irregularly polygonal to meandroid corallites, and its tabulae are flattened to undulating and complete. The form has a general resemblance with corallites and tabulae as analogues of the pillars and cyst plates in stromatocid stromatoporoids, but marked differences exist in preservational states of the two groups. The compound, modular, coralomorph colonies and stromatocid stromatoporoid skeletons belong to completely unrelated groups of organisms, yet apparently each group was still capable of producing convergently similar skeletal structures in response to their respective growth in temporally discrete and independent reef-building episodes.

**Coralomorph Genera *Khasaktia*  
SAYUTINA, 1980, *Vittia* SAYUTINA, 1980,  
and Others**

These small, problematical early Cambrian genera were first described as members of a new family, the Khasaktiidae of SAYUTINA (1980), and suggested to have affinities with Paleozoic stromatoporoids (see also SAYUTINA in VORONIN & others, 1982, p. 66–68, pl. 8, 6–9, pl. 9, 1–8; SAYUTINA, 1983, p. 149–151, pl. 30, 1–5, pl. 31, 5; WEBBY, 1986, p. 150; WEBBY in STEARN & others, 1999, p. 59–61; and SCRUTTON, 1997, p. 196, for further discussions). Compared with stromatoporoids, these forms are a rather heterogeneous group, with structures that have finer and smaller sizes. The crustlike genera *Khasaktia* and *Vittia* were considered by ROZANOV and ZHURAVLEV (1992, p. 230) to have been archaeocyath holdfasts (see also NESTOR in STEARN & others, 1999, p. 60), and some crusts of *Vittia* were noted

(WEBBY, 1986, p. 150, fig. 2B) to be similar to certain labechiids, but the relationship is almost certainly to be convergent. The dendroid, multilayered *Edelsteinia* VOLOGDIN, 1940a, *Rackovskia* VOLOGDIN, 1940a, and *Drosdovia* SAYUTINA, 1980, were thought likely, especially based on their microstructures, to be coralomorphs (DEBRENNE, LAFUSTE, & ZHURAVLEV, 1990; ROZANOV & ZHURAVLEV, 1992; ZHURAVLEV, 2001c). However, RIDING (2001, p. 452) suggested *Edelsteinia* as an alga.

Others, for example, WRONA & ZHURAVLEV (1996 p. 31), PRATT & others (2001, p. 260), and DEBRENNE & REITNER (2001, p. 315) have recorded the family Khasaktiidae as a junior synonym of the family Tannuolaiidae VOLOGDIN, 1967. Their decision was apparently based on resemblances between VOLOGDIN's (1967) new genus and type species, *Tannuolaia fonini*, from an early Cambrian sequence in southern Tuva (Russia), and SAYUTINA's (1980) khasaktiid taxa described from the Siberian Platform and Mongolia, especially the close morphological similarities between *T. fonini* and the "khasaktiid" genus *Edelsteinia*.

However, relationships between the two families Tannuolaiidae and Khasaktiidae still need to be more fully explored. For example, VOLOGDIN (1967) interpreted the tannuolaiids as green algae (Chlorophyta), whereas SAYUTINA (1980) treated the superficially similar early Cambrian khasaktiids as skeletonized structures of stromatoporoid-type (likely to be derived from either sponge or cnidarian lines of descent) or, alternatively, having uncertain origins, as implied by BOGOYAVLENSKAYA (1984, 2001a). Also, SCRUTTON (1997, p. 196, 199) has reviewed some of the khasaktiid taxa in terms of possible cnidarian relationships, indicating that they are unlikely to be related, apart from one genus, *Rackovskia*, which could be viewed as a zoantharian coral. SCRUTTON (1997) also commented on other forms such as *Khasaktia*, which he found difficult to assess: he preferred

to keep an open mind on its relationships until this genus, and all the other problematical, skeletonized, early Cambrian life forms discussed here, were much more intensively studied to clarify their precise nature, origins, interrelationships, and patterns of diversification.

BOGOYAVLENSKAYA (2001a, p. 46) also proposed the new order Khasaktiida of class *Incertae Sedis* (note the original “-ida” ending is here amended to an “-iida” ending to maintain consistency with the formalized family ending of the Khasaktiidae, discussed above). She only incorporated family Khasaktiidae, with the genera *Khasaktia* and *Vittia*, in her new order, and she also arbitrarily assigned a number of the major groups of stromatoporoids to this artificial grouping as well, including such orders as the Labechiida, Clathrodictyida, and Actinostromatida in her conception of class *Incertae Sedis*. Later, BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA & YELKIN, 2011, p. 15–20) combined the khasaktiid order and the above-mentioned stromatoporoid orders again into one group, but this time she referred them all to the class Hydrozoa within the phylum Cnidaria (=Coelenterata). Again, this appears to have been a rather arbitrary change, though perhaps best explained in terms of her earlier views (see BOGOYAVLENSKAYA, 1984, fig. 16) that all stromatoporoid orders had affinities to hydrozoans. For additional comments on other aspects of Bogoyavlenskaya’s stromatoporoid-based classifications (BOGOYAVLENSKAYA, 1984, 2001a; BOGOYAVLENSKAYA & YELKIN, 2006, 2011; also see p. 581–583, 702).

Nevertheless, it remains unlikely that the problematical early Cambrian khasaktiids (based on *Khasaktia* and *Vittia*) were closely related to the Mid-Ordovician to Devonian stromatoporoids. The two groups do show convergently similar skeletal features, but they are phylogenetically remote from each other, given the approximately 60 myr gap in the record of occurrences. Also the khasaktiids have relatively restricted occurrences

within Siberia, Mongolia, and West Antarctica, and they lack astrorhizal structures.

#### Problematical Genus *Maldeotaina* FLÜGEL & SINGH, 2003

In another example from a richly fossiliferous, nodular, limestone sample near the top of the Krol Formation (close to the Precambrian–Cambrian boundary) of northern India, two associations were recorded as including the presence of morphologically differentiated calcified sponges, with one (*Maldeotaina*) thought to include an example of stromatoporoid-like growth (FLÜGEL & SINGH, 2003, pl. 66, 1). The form genus *Maldeotaina* comprises centimeter-sized nodules, including a stromatoporoid-like component that appears to have overgrown areas that were formerly voids (possibly original cavities). These exhibit lighter, spar-filled, vesicular, early marine cement botryoids, and each seems to be defined by a thin, dark, much-crenulated encrustation of microbial micrite. FLÜGEL and SINGH’s (2003, p. 369) view, that this vesicular, inner part of the nodule was part of sponge “thalamid-type growth” is here rejected in favor of an interpretation that it was, more likely, formed mainly by the precipitation of early marine cements. The stromatoporoid-like overgrowth is a fine meshwork of rodlike and cystlike elements that resembles some examples of fine-textured labechiid stromatoporoids, and, in one part of the skeleton where it continued to grow, it developed a columnar growth form with an internal phase change to predominant cyst rows (FLÜGEL & SINGH, 2003, p. 366, pl. 66, 1). In contrast to the *Maldeotaina* overgrowths, the skeletons of fine-textured labechiids, like members of the *Labechia prima* group and species of *Stratodictyon* (KAPP & STEARN, 1975; WEBBY, 1979a), exhibit less variability in their cystlike sizes and shapes; a more regular arrangement of cyst rows; rodlike (pillar) elements that do not show a tendency to become amalgamated in their outer zones; and do not exhibit similar patterns of encircling,

encrusting meshworks around small nodules. Typically, labechiids form laminar skeletons and commonly have associated latilaminae. Consequently, the *Maldeotaina* overgrowth structure, though it superficially resembles fine-textured labechiid stromatoporoids, is likely to belong to some other early Cambrian form, perhaps a new variety of cyanobacterium or alga. Alternatively, the stromatoporoid-like part of the structure may represent another khasaktiid genus. Whichever alternative is favored, the simple, calcified skeleton lived more than 60 myr before phylogenetically unrelated, and convergently similar, labechiid stromatoporoids.

#### MID-CAMBRIAN TO EARLY ORDOVICIAN GAP IN THE RECORD

No stromatoporoid-like skeletal structures have been reported from reef or other habitats of the mid-Cambrian to Early Ordovician (Tremadocian). According to ROWLAND and SHAPIRO (2002, p. 119), the reef settings were almost entirely dominated by microbialite-building cyanobacteria, which had opportunistically invaded as metazoans disappeared, owing to seawater chemistry changes (a reduction in the Mg/Ca ratio prevented organisms that secreted high Mg calcite or aragonite skeletons [STANLEY & HARDIE, 1998]). Other factors, such as global warming, high levels of atmospheric CO<sub>2</sub>, and the nutrient deficiencies of marine environments may have contributed also, directly or indirectly, to inhibiting the development of metazoan reef builders (ROWLAND & SHAPIRO, 2002, p. 95).

#### EARLY TO MID-ORDOVICIAN PULCHRILAMINIDA: AN INDEPENDENT, REEF-BUILDING HYPERCALCIFIED SPONGE

The small, geographically relatively restricted group of pulchrilaminid hypercalcified sponges appeared in North American

(Laurentian) successions during the late Early Ordovician (Floian Stage; see BERGSTRÖM & others, 2006), forming important frame-building contributors to reef mounds, especially the upper parts of the mounds, and in some forms, they also exhibit fine spicule-like elements aligned in palisade bands (Fig. 358). Best documented were the *Pulchrilamina*-bearing reef mounds in Texas and Oklahoma (TOOMEY & HAM, 1967; TOOMEY, 1970; TOOMEY & NITECKI, 1979; TOOMEY & BABCOCK, 1983; WEBBY, 1986, 2002, p. 140). *Pulchrilamina* has also been reported from bedded sequences of Floian age (PRATT & JAMES, 1989), and reef-derived clasts of lower Mid-Ordovician (Dapingian) age (POHLER & JAMES, 1989) in Newfoundland.

Also, in places, pulchrilaminids are represented mainly by sheetlike encrustations, and these may also be furnished with spicule-bearing palisade bands, as in the Lower Ordovician (upper Tremadocian–lower Floian) successions of Hubei Province, southern China (ZHU, LIU, & LI, 1993; ADACHI, LIU, & EZAKI, 2011), and there are more doubtful records of pulchrilaminids, given that they lack the palisade-bearing, fine spicule-like elements occurring in the Middle Ordovician—the genus *Zondarella* KELLER & FLÜGEL, 1996, from the reef and biostromes of the Dapingian (lower Mid-Ordovician) of the Argentine Precordillera (that was possibly derived originally as a microcontinental block from near the Ouachita embayment in the southeastern United States; THOMAS & ASTINI, 1996; KELLER, 1999), and the genus *Ianilamina* PICKETT & ZHEN in ZHEN & PICKETT, 2008, from the lower Darriwilian (middle Mid-Ordovician) of central New South Wales, Australia, that formed as an isolated occurrence in a Darriwilian limestone lens of a volcanic arc setting in eastern Australia.

TOOMEY and HAM (1967, p. 984) reviewed the status of their enigmatic new genus *Pulchrilamina*, concluding that the genus should be assigned to *Incertae Sedis*, possibly a “primitive coelenterate,” akin to stromato-

poroids. This view was formed when stromatoporoid workers were still interpreting stromatoporoids as hydrozoans. However, from the 1970s onward, as the views of HARTMAN and GOREAU (1970, 1972, 1975) linking living hypercalcified sponges and fossil stromatoporoids gained acceptance, some workers did interpret *Pulchrilamina* as a sponge (e.g., PRATT & JAMES, 1982). Nonetheless, few stromatoporoid specialists have included *Pulchrilamina* in their surveys of stromatoporoids since the 1970s, either because they were unaware of the existence of this small, comparatively restricted group, or because they doubted the group had links to stromatoporoids (e.g., STEARN, 1980; BOGOYAVLENSKAYA, 1984; BOGOYAVLENSKAYA & LOBANOV, 1990; KHROMYKH, 1999a, 1999b).

*Pulchrilamina* was first described by TOOMEY and HAM (1967) as being formed of large, domical-shaped skeletons with wavy, sheetlike layers (laminations) and erect, upward, sharply pointed spines (spinose rods) that rise above the tops of individual layers into the intimately associated wedges or layers of mudrock; both sheets and centers of the spines are invariably replaced by sparry calcite. Later, TOOMEY and NITECKI (1979, fig. 13) identified small areas of the predominantly spar-replaced sheets as being composed of rows of gently wavy, cyst-like laminae that formed meshworks with the upright, spinelike rods, but they did not offer further comment on the possible significance of these morphological features.

STEARNS (1972, p. 374) drew attention to *Pulchrilamina* in a comparison between gross structures of living hypercalcified sponges and Paleozoic stromatoporoids, such as the densely thickened Silurian genus *Lophiostroma*, apparently because it was thought to be composed of a solid mass of calcite. NESTOR (1978) and SAYUTINA (1980) also gave credence to the linkage between *Pulchrilamina* and the skeletally dense, massively thickened members of the family Lophiostromatidae NESTOR, 1966a, favoring a view that *Pulchrilamina* may have been the

ancestor of the Stromatoporoida, through a lophiostromatid line of descent. STOCK (1983, p. 167) was another who commented on the close morphological similarities between skeletal structures of *Pulchrilamina* and the labechiids, recommending that further comparative studies of relationships were needed.

Studies of *Pulchrilamina* in the 1980s led to initial suggestions by WEBBY (1984a, p. 91; 1984b, p. 200) that the generalized growth form, latilaminae, cysts, and pillars were similar to later Ordovician labechiids. However, in a more detailed account, WEBBY (1986, p. 151–154, fig. 3–4) noted that, while there were mainly no substantial differences between the genus *Pulchrilamina* and members of the family Labechiidae, the pattern of long, slender, spinose rods (or spicules) extending above the tops of latilaminae in palisade bands was not typical of the Labechiidae. At this time (WEBBY, 1986, p. 154–155, fig. 5), *Pulchrilamina* was still depicted as a possible ancestor to other late Middle Ordovician genera of order Labechiida and the family Labechiidae. But later, WEBBY (1993, p. 58; 1994, p. 375) erected the family Pulchrilaminidae to accommodate the genus *Pulchrilamina*, retaining it with some reservations in the order Labechiida, because the long-low cysts had limited lateral continuity and the spinelike and sometimes tilted nature of the long, slender spicule-like elements suggested a much more loosely aggregated skeleton than in typical labechiids. Two other general concerns were discussed: (1) whether *Pulchrilamina* was truly ancestral to later members of the order Labechiida, given the above-stated morphological differences; or (2) whether, alternatively, the apparent close relationships arose merely as a consequence of convergences between pulchrilaminids and labechiids and were two unrelated groups (Fig. 358). A similar viewpoint was offered by WEBBY (in STEARN & others, 1999, p. 23) in recognizing the family Pulchrilaminidae as a doubtful member of the order Labechiida, or a small,

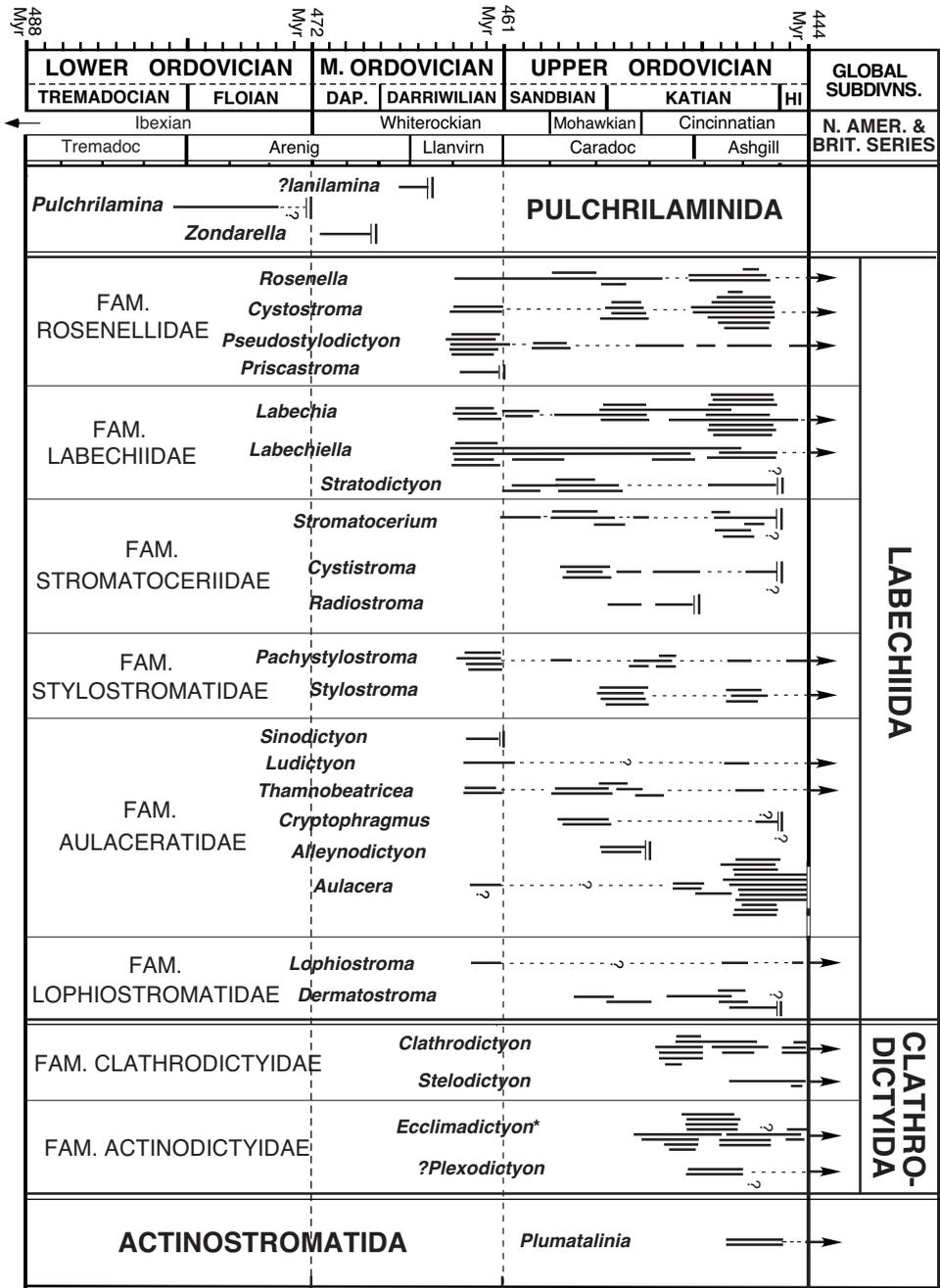


FIG. 358. (For explanation, see facing page).

unrelated, early, reef-forming group. By using a revised Ordovician time scale, WEBBY (2004b) suggested that a gap of about half the length of the Darrwiliian stage (about 4 myr) separated the last appearance of mainly Laurentian pulchrilaminids and the first, sudden, mass appearances of labechiid stromatoporoids worldwide (distributed across paleoequatorial carbonate shelfal regions of North America, Siberia, northern China, Southeast Asia, and Australia). However, the recent discovery of the short-lived *Ianilamina* in the lower Darrwiliian of Australia suggests now that there was no substantial gap in time between the last appearance of pulchrilaminids and the first appearances of indubitable labechiids.

WEBBY (p. 837–844) proposed the new order Pulchrilaminida to accommodate the eponymous family Pulchrilaminidae WEBBY, 1993. The order is regarded as a separate, independent group of hypercalcified sponges, placed in class Uncertain. Given its distinctive, slenderly tapering, rodlike, spicular elements that resemble styles, it may be more closely linked to spiculate sponge groups of the class Demospongiae than to nonspiculate stromatoporoid groups. In conclusion, it seems that much of the early history of pre-labechiid, spongelike forms, like the Pulchrilaminida, is not recorded in known fossils. The order Pulchrilaminida is a small clade with poriferan affinities that has a limited geographic spread and evolved as a reef-former in parts of North America, the Argentine Precordillera, and in southern

China during the late Early Ordovician, surviving as reef-formers, at least to the end of the early Middle Ordovician. Additionally, there are records of pulchrilaminids as encrusters or matlike forms in most of the same places, but they also seem to have appeared earlier in the late Tremadocian of southern China, as well as surviving longer in certain places, like the isolated occurrence of problematic *Ianilamina* in a Darrwiliian limestone lens of a volcanic arc setting in eastern Australia. Though it appears morphologically close to the Argentine *Zondarella* KELLER & FLÜGEL, 1996, it differs, according to PICKETT and ZHEN (in ZHEN & PICKETT, 2008, p. 66), in exhibiting “porous laminae,” a feature that they believe implies a relationship with nonlabechiid ?clathrodictyid-type stromatoporoids. However, the genus *Ianilamina* has no direct link with the order Clathrodictyida, which first appeared some 10 myr later, during the Late Ordovician (Katian) age (see p. 590).

BOGOYAVLENSKAYA’S (2001a, p. 46) proposal of the order Protolabechiida of class *Incertae Sedis* to accommodate a heterogenous assortment of labechiid, lophiostromatid, and pulchrilaminid families (and genera) is here rejected in favor of separating them into two clearly differentiated orders: the Pulchrilaminida and the Labechiida. Arguments against adopting the order Protolabechiida as a valid taxonomic subdivision are presented elsewhere (see separate sections on the taxonomy of the Labechiida, p. 709–754, and the Pulchrilaminida, p. 837–844).

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FIG. 358. Chart showing temporal ranges of Ordovician stromatoporoids (orders Labechiida, Clathrodictyida, and Actinostromatida) and the problematical order Pulchrilaminida, worldwide, based on the sampled record. The named genera are represented with clusters of vertical lines representing approximate numbers of species and their ranges within a genus; dotted vertical lines represent gaps in the continuity of record, and the double cross bars depict inferred levels of extinction of individual genera; note the abbreviations of global subdivisions: DAP (Dapingian stage) and HI (Hirnantian stage). The pattern of first appearances commences with the major radiation of 12 labechiid genera in the late Middle Ordovician, then successive smaller pulses involving *Stratodictyon* and *Stromatocerium* near the mid–Late Ordovician boundary, followed by *Cystistroma*, *Cryptophragmus*, and *Dermatostroma* in the mid-Sandbian (early Upper Ordovician), then *Radiostroma*, *Stylostroma*, and *Alleynodictyon* near the Sandbian–Katian boundary. The clathrodictyids (4 genera) radiate later, during the mid–Late Ordovician (Katian), possibly from a *Cystostroma*-like ancestor; asterisk, the genus *Ecclimadictyon* is now separated into two genera, with the addition of newly designated genus *Camptodictyon* NESTOR, COPPER, & STOCK (2010, p. 84), including a distinctive Ordovician species. Also, the first actinostromatid (*Plumatalinia*) evolved in the late Katian, probably from a species of *Pseudostylocdictyon* (adapted from Webby, 2004b, fig. 13.1; with permission of Columbia University Press, New York).

There is also a superficially similar hypercalcified spongelike organism of large size in the Table Head Formation of western Newfoundland, of lower Mid-Ordovician (Dapingian) age. It has a form that is not referable to stromatoporoids, chaetetids, secondarily altered lithistid sponges, or cryptalgal structures. This problematical taxon, described as *Lapidipanis terranova* PAQUETTE, STEARN, & KLAPPA, 1983, exhibits a spherulitic microstructure that has led to the suggestion that it may have links with living (and Triassic) hypercalcified demosponge *Astroclera* LISTER, 1900 (see p. 5). However, the spherules in *Lapidipanis* are larger than those found in *Astroclera* (VACELET, 2002a, p. 825).

### THE LABECHIIDAE: RECORD OF EARLIEST STROMATOPOROIDS

In terms of the classification of the order Labechiida employed in this volume of the *Treatise on Invertebrate Paleontology*, it follows relatively closely the taxonomic framework used previously by WEBBY (see STEARN & others, 1999). The only significant differences are the exclusion of the family Pulchrilaminidae WEBBY, 1993, which was previously included with some uncertainty, and the Stromatoceriidae BOGOYAVLENSKAYA, 1969b, now divided into two families (comprising the revised Stromatoceriidae and Platiferostromatidae YAVORSKY in KHALFINA & YAVORSKY, 1973). The order Labechiida here comprises seven families: Rosenelliidae (six genera), Labechiidae (three genera), Stromatoceriidae (three genera), Platiferostromatidae (five genera), Stylostromatidae (five genera), Aulaceratidae (seven genera), and Lophiostromatidae (two genera). Six of these, all except the Platiferostromatidae, have an Ordovician record (Fig. 358) for labechiids; see also the Paleozoic record of Labechiida (Fig. 362). The family Cystostromatidae KHROMYKH, 1974a, has not been accepted by other workers; its included taxa comprise a heterogeneous mixture of forms that should be assigned

to at least three different labechiid families: Rosenelliidae, Labechiidae, and Stromatoceriidae (and all of these family names have priority over KHROMYKH's Cystostromatidae). This latter family was referred by KHROMYKH (1999b) to the order Clathrodictyida, thus confusing its true identity. It does not show diagnostic features of clathrodictyids—that is the presence of single-layered, inflected to planar laminae and short to superposed pillars (see p. 755). Therefore the use of family Cystostromatidae and the order Cystostromatida (see KHROMYKH, 2001, p. 344) should be abandoned.

A well-constrained, globally based, stratigraphic framework (SADLER & COOPER, 2004; WEBBY, COOPER, & others, 2004; BERGSTRÖM & others, 2009; SADLER, COOPER, & MELCHIN, 2009) has become available to assess the origins and evolutionary development of the group. Earlier attempts to review this topic (WEBBY, 1979a, 1993; BOGOYAVLENSKAYA & LOBANOV, 1990; KHROMYKH, 1999b) were hampered by the difficulty of establishing precise ties between the local and regional range data and the available, globally based time scales.

BOGOYAVLENSKAYA (2001a, p. 48–49) and BOGOYAVLENSKAYA and YELTIN (2006, p. 188–189) adopted a classification of the order Labechiida that included six families, with four of these (“Rosenelliidae,” Labechiidae, Aulaceratidae, and Stromatoceriidae) bearing some similarity to the familial subdivisions used in the present classification but with the two other families (Cystostromatidae and Tuvaechiidae) having markedly different conceptions. Nevertheless, the order was maintained with the scope of a major stromatoporoid group. However, BOGOYAVLENSKAYA and YELTIN (2011, p. 19) have since added a radically different proposal that greatly restricts the conception of the order Labechiida, in removing all the previously adopted families except the Labechiidae. This drastically alters the understanding of labechiids as a major, essentially unified, stromatoporoid group through the Mid-Ordovician to Late Devo-

nian, comprised of a comparatively simple skeletal meshwork of cyst plates and rounded to flanged pillars, and/or denticles. The traditional conception must be maintained; and hence the BOGOYAVLENSKAYA and YELTIN (2011) proposal must be rejected.

In a survey of Ordovician diversity trends, WEBBY (2004b) demonstrated that the labechiid stromatoporoids first appeared quite suddenly in the late Middle Ordovician (mid-late Darriwilian age), associated with a significant global evolutionary event. It involved the initial differentiation of 5 of the 7 labechiid families, with the appearance of 12 genera (i.e., representing a little less than half the known labechiid genera in the fossil record). It appeared that this event was concentrated in low paleolatitudes, mainly in shallow carbonate platform and shelf (including reef) sites of Laurentia, Siberia, and eastern Asia. Other metazoans, such as corals and bryozoans, and algal components also diversified rapidly at this time, and many new and complex reef community associations became established, as well as significant increases of bioeroders, encrusters, and bioturbators associated with the reef (WEBBY, 2002, 2004a). The reef-building phase is best developed in Laurentia, in particular, as seen in the eastern North American Chazyan reefs.

The globally distributed, mid-late Darriwilian, labechiid genera are distributed across five of the six known Ordovician families (see Fig. 358). The family Rosenellidae includes four genera (*Rosenella* from northern China [NC], Korea [K], and Malaysia [M]; *Cystostroma* from eastern North America [ENA]; *Pseudostylodictyon* from ENA and NC; and *Priscastroma* from Siberia); family Labechiidae includes two genera (*Labechia* from ENA and NC; and *Labechiella* from NC, K, and M), family Stylostromatidae includes one genus (*Pachystylostroma* from ENA), family Aulaceratidae includes four genera (*Aulacera*, *Thamnobeatricea*, *Sinodictyon*, and *Ludictyon* from NC); and family Lophiostromatidae includes

one genus (*Lophiostroma* from NC). It should be noted that none of these early labechiid genera exhibits a circumpaleoequatorial distribution. A few occur in two main regions (e.g., *Pseudostylodictyon* and *Labechia* in ENA and NC), but all others (10 genera) have a largely restricted regional distribution, either in ENA, eastern or southeastern Asia (i.e., NC, or NC, K, and M), or in Siberia. It seems likely, therefore, that an initial simple, noncalcifying rootstock existed in warm shallow seas of most paleoequatorial regions, and then the mineralized skeletons of a number of different basic morphologies developed, most of them in comparative isolation to each other, either directly related to a globally widespread environmental perturbation or independently of it. The alternative is to suggest that one or two basic skeletonized morphologies of *Cystostroma*- or *Pseudostylodictyon*-type evolved first in the mid-Darriwilian and then spread circumequatorially over the next one to three million years, prior to the end of Mid-Ordovician time.

The events associated with the first appearances of stromatoporoid-bearing Chazyan reefs (Day Point to Crown Point formations) in eastern North America (KAPP & STEARN, 1975) were apparently mirrored by dramatic diversity changes in the contemporaneous, mainly level bottom communities of the Siberian Platform (KANYGIN, 2001), and, by the first appearance of the labechiid genus *Priscastroma* KHRAMYKH, 1999a, in the Moiero River basin section of that platform sequence. The stromatoporoid-bearing sequences in northern China and other parts of Asia were all of similar mid-upper Darriwilian age (WEBBY, 2004b, p. 114). Most of the early labechiid occurrences in northern China come from horizons in upper parts of the Machiakou Formation or its equivalents (YABE & SUGIYAMA, 1930; DONG, 1982; LIN & WEBBY, 1989), and they broadly correlate with the middle upper Llanvirn interval, i.e., they represent a mid-upper Darriwilian age (see Chinese correlation chart in CHEN & others, 1995).

Two additional genera, *Stratodictyon* (family Labechiidae from ENA and Australia [Tasmania and New South Wales]) and *Stromatocerium* (the type genus of the sixth labechiid family, the Stromatoceriidae from Australia [Tasmania]) have first appearances near the Middle–Upper Ordovician boundary. The Chazy Group succession apparently straddles the boundary with the Day Point and Crown Point formations in the uppermost Darriwilian and the overlying Valcour formation in the lowest Sandbian (see WEBBY, 2002, fig. 6). *Stratodictyon valcourensis* (KAPP & STEARN, 1975) first appears in the Valcour Formation of the upper Chazy Group and is therefore lower Sandbian in age (BERGSTRÖM & others, 2006). In Australia, there are records of *S. vetus* WEBBY, 1979b, in Tasmania and in New South Wales (PICKETT & PERCIVAL, 2001), and the New South Wales occurrence comes from a horizon a few hundred meters above the key zonal conodont marker, *Pygodus anserinus*, which identifies the boundary interval; hence the *S. vetus* outcrop is of lowest Sandbian age. The occurrence of *Stromatocerium bigsbyi* in Tasmania is associated with *S. vetus*, so this stromatoporoid-rich succession also is probably younger than previously thought (WEBBY, 1979b, fig. 1), still correlating with the upper part of the Chazy Group sequence but within beds now considered to lie just above the Middle–Upper Ordovician boundary.

The labechiid origins through the rest of the Late Ordovician are limited to a few new genera that appeared at intervals from late Sandbian to early Katian (early–mid Late Ordovician) time (BERGSTRÖM & others, 2006). These included *Cystistroma* (family Stromatoceriidae) and *Cryptophragmus* (family Aulaceratidae) from the late Sandbian, and *Dermatostroma* (family Lophiostromatidae), *Stylostroma* (family Stylostromatidae), *Radiostroma* (family Stromatoceriidae), and *Alleynodictyon* (family Aulaceratidae), from the early Katian (Fig. 358). All of these genera are likely to have been derived from one

or another of the existing skeletonized, mid–late Darriwilian, labechiid taxa. A maximum of 20 labechiid genera occur in the Late Ordovician. At the species level, the labechiids also became most diversified in the Late Ordovician, as they spread more widely circumequatorially along platforms, shelf margins, and in island arcs than previously. Of particular note is the marked diversification of columnar aulaceratids, up to 13 species of *Aulacera* recorded from the uppermost Ordovician (upper Katian to Hirnantian) worldwide, prior to their end-Ordovician mass extinction. In North American successions in particular, the diversity decline of labechiid genera into the early Silurian is most noticeable (NESTOR & STOCK, 2001, fig. 1).

BOGOYAVLENSKAYA and LOBANOV (1990) adopted a different approach to determining early origins, using a combination of stratigraphic distributions, zoogeographic patterns, and apparent phylogenetic relationships. They reviewed the diverse labechiid assemblage in the Chazy Group, giving some of them different names from the taxa adopted here. For example, *Pseudostylodictyon* OZAKI, 1938, was subdivided into two genera (*Pseudostylodictyon* and *Parksodictyon* BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & LOBANOV, 1990); however, this discrimination based solely on one taxonomic character (presence or absence of mamelon columns) seems inadequate for recognizing such a genus-level subdivision and is rejected here (see p. 709–754). *Parksodictyon* has been revised as a junior synonym of *Pseudostylodictyon*. Also, genus *Tuvaechia* BOGOYAVLENSKAYA, 1971b, which she used in preference to *Labechia* EDWARDS & HAIME, 1851, or *Labechiella* YABE & SUGIYAMA, 1930, for identifying some Chazy forms, is now considered to be a junior synonym of *Labechiella* (see p. 709–754). BOGOYAVLENSKAYA and LOBANOV's (1990, fig. 3) Middle Ordovician (Llanvirn–Llandeilo) was largely equivalent to the late Mid-Ordovician (mid–late Darriwilian interval) but is now established in the well-

constrained global time scales of BERGSTRÖM and others (2009) and SADLER, COOPER, and MELCHIN (2009) as representing a duration of about 5 myr, and the Late Ordovician interval is recognized as having a much longer duration of about 17 myr.

A summary of BOGOYAVLENSKAYA and LOBANOV's phylogenetic scheme for the mid-late Darriwilian interval comprised three main lines of descent. The first involved initial appearance of so-called "*Parksodictyon*" in the mid-late Darriwilian, then divergence into two branches involving *Pseudostylodictyon* and *Stratodictyon* in the latest Darriwilian; though the first appearance of *Stratodictyon* was probably later in the Sandbian (earliest Late Ordovician), given the earliest North American and Australian records (see earlier discussion, p. 583). The second line included the appearance of "*Tuvaechia*" (= *Labechiella*), with *Stromatocerium* as an offshoot in the latest Darriwilian, but again this offset probably did not occur until much later, in the earliest Late Ordovician. The third line of descent involved *Cystostroma* and *Pachystylostroma*, with these 2 genera appearing and diverging immediately, approximately latest Darriwilian time. The *Cystostroma* offshoot gave rise to many of the aulaceratid genera later in the Ordovician, and apparently to clathrodictyids as well. Overall, BOGOYAVLENSKAYA and LOBANOV's (1990, fig. 3) phylogenetic tree is one of a steplike build up of new taxa through late Middle Ordovician to Late Ordovician time. They identified a maximum of 7 taxa by the end of the Middle Ordovician and a maximum of 12 genera in the mid-to-late Late Ordovician (late Katian), followed by rapid decline associated with the end-Ordovician extinction. Only 2 genera are recorded from the early Silurian.

KHROMYKH (1999b) also attempted to establish the main patterns of origins and early development of stromatoporoids, employing generalized stratigraphic distributions and inferred phylogenetic relationships to determine evolutionary trends, with

global correlations using a broadly based time scale with subdivisions from a general stratigraphic scale using older (pre-1995) British standard series names. KHROMYKH (1999b) correlated the base of his Middle Ordovician with the base of the Llanvirn, which equates with a position in the current global Ordovician time scale similar to the middle of the Middle Ordovician series, i.e., in the lower half of the Darriwilian stage (WEBBY & others, 2004). KHROMYKH (1999b, table 1) provided stromatoporoid distribution data ranging from the topmost Mid-Ordovician (mid-upper Darriwilian) through to the mid-Upper Ordovician (mid-Katian stage = British late Caradoc), i.e., through about 15 myr of Earth history. KHROMYKH (1999b, fig. 1–2) presented a summary of the distribution of taxa from a phylogenetic point of view and a stratigraphic chart also showing the stepwise increase of generic diversity through late Mid- to mid-Late Ordovician time.

The mid-late Darriwilian record represents an interval of about 5 myr, and in KHROMYKH's (1999b) phylogenetic tree, the Siberian genus *Priscastroma* (type species *P. gemina*, with two varieties "a" and "b" (= forma A and B) were considered to be ancestral to other early stromatoporoids. The two varieties were recognized as the basis for a number of lines of descent, a main branch from *P. gemina* var. "a" leading to *Cystostroma*, then three separate offsets, in the first branch to *Stromatocerium*, *Pachystylostroma*, and "*Parksodictyon*," this latter becoming *Pseudostylodictyon* by the end of the Middle Ordovician (end-Darriwilian), and a second branch in the early Late Ordovician producing *Rosenella* by the early Katian, and then *Clathrodictyon* on another branch in the mid-Katian. An additional side branch from *P. gemina* var. "a" gave rise to *Dermatostroma* in the early Katian, and the two offshoots from *P. gemina* var. "b" apparently produced *Labechia* in the latest Darriwilian and *Lophiostroma* in the early Sandbian. This overall coverage of labechiid and clathrodictyid genera (KHROMYKH, 1999b, fig. 2) included

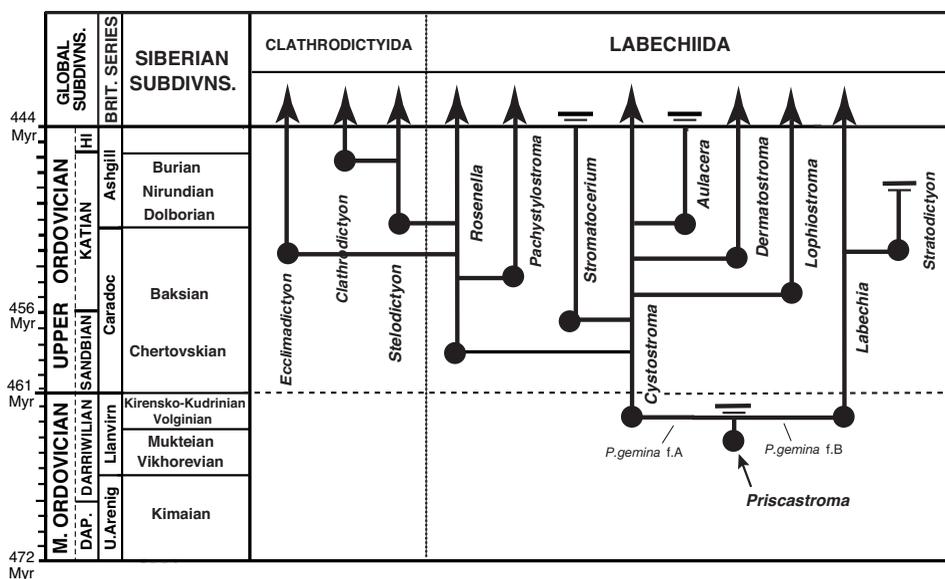


FIG. 359. Chart showing the inferred evolutionary relationships of 13 Mid–Late Ordovician stromatoporoid genera (10 labechiids, 3 clathrodictyids) from the Siberian Platform and Taymyr Peninsula (northeastern Siberia), based on data assembled by KHROMYKH (2010). The ranges of individual genera are shown by thickened vertical lines from their earliest records (denoted by black circles); double cross bars represent inferred levels of extinction, and upwardly directed arrows indicate taxa that have extended ranges above the Ordovician–Silurian boundary; note the abbreviations of global subdivisions: DAP (Dapingian stage) and HI (Hirnantian stage). The initial radiation of genus *Priscastroma* is based on type species *P. gemina*, which produced two variants (forma “A” and “B”) thought by KHROMYKH (2010) to be ancestral to different lines of descent involving *Cystostroma* and *Labechia*, respectively. Two genera from the Upper Ordovician of Taymyr, *Nestoridictyon* KHROMYKH, 2001, and *Taymyrostroma* KHROMYKH, 2001, are excluded from this plot, because the first is considered to be a junior synonym of *Stromatocerium* (see p. 725), and *Taymyrostroma* has been classified by STEARN (2011b, p. 49–56; and see p. 829–836) in a stromatoporoid order and family with uncertain affinities (Webby, 2012b).

11 genera, which contrasts with the much larger total of genera known globally—some 24 genera plotted in Figure 358.

In a second contribution on the early evolution of stromatoporoids, KHROMYKH (2010) adopted a different approach, documenting the Ordovician and Silurian stromatoporoid generic records of the epicontinental so-called paleobasin successions of the Siberian Platform and the Taymyr Peninsula. Attention was focused on two important composite sections through the Ordovician (another included the Silurian record but is not considered here), including the Middle to Upper Ordovician succession in the Siberian Platform, and through the Upper Ordovician sequences of the other composite section in Taymyr. KHRO-

MYKH (2010, fig. 2–3) compiled data in two stratigraphic columns, with details of the regional stratigraphic framework, tentative ties with global stage subdivisions, lithological details, thicknesses, stromatoporoid-bearing intervals, and first appearances of named genera. The total thickness of the Siberian Platform composite section is 130 m thick, and it has stromatoporoid-bearing limey deposits occupying about 38% of the total sequence, while the total thickness of the Taymyr composite section is 327 m thick and the stromatoporoid-bearing limey deposits comprises about the same proportion of the total sequence. In the Siberian Platform, the first appearances of sampled genera through the Mid–Upper Ordovician are as follows: *Priscastroma* and *Cysto-*

*stroma* in the mid–upper Darriwilian, then *Stromatocerium*, *Lophiostroma*, *Rosenella*, *Pachystylostroma*, and *Labechia* in Sandbian equivalents, followed by *Aulacera* in the mid-Katian. In the Taimyr Peninsula, first appearances of genera include the following, in stratigraphic order: from lower Katian (*Stratodictyon*, *Stelodictyon*, and *Ecclimadictyon*), to mid-Katian (*Dermatostroma*), and finally to Hirnantian (*Clathrodiction*).

Most of the above-mentioned genera were included in an Ordovician–Silurian phylogenetic tree of KHROMYKH (2010, fig. 4) that displays only the generic data from the Siberian region. A compilation based on KHROMYKH's data is presented here, showing a phylogeny just for the Ordovician part of the Siberian record (see Fig. 359); its purpose is to allow comparisons between the generalized worldwide– and regional (Siberian)–based Ordovician plots presented in Figures 358 and 359. Based on the Siberian record, most of the genera, excepting *Labechia* and *Stratodictyon*, were derived directly or indirectly from *Cystostroma* (KHROMYKH, 2010, p. 691). *Cystostroma* initially gave rise to *Rosenella*, and then two side branches from *Rosenella* led directly to the first members of the Clathrodictionida; that is, *Ecclimadictyon* and *Stelodictyon* during the mid-Katian, and then *Clathrodiction* was derived from *Stelodiction* in the late Katian. All the other genera are members of the Labechiida (Fig. 359).

KHROMYKH (2010, p. 691) considered that all the Siberian taxa found in the Ordovician deposits had originated in the Siberian paleobasin; and he specifically named *Cystostroma*, *Dermatostroma*, *Pachystylostroma*, and *Stromatocerium* as genera that emerged earlier in the Siberian paleobasin than in other basinal regions elsewhere in the world. He did not discuss matters such as whether any of the Siberian faunal elements might have originated in other parts of the world, then migrated later into the Siberian region. Such a conclusion, however, must be drawn from comparing the patterns of first appearances of genera in the global and the Siberian charts (Fig. 358–359). For example, the

labechiid genera *Pachystylostroma*, *Lophiostroma*, *Stratodiction*, and *Aulacera* all exhibit earlier appearances, based on comparing the data plotted globally (Fig. 358) and regionally within Siberia (Fig. 359), and this implies that at least these four genera may have migrated initially into the Siberian region, rather than first evolving within the Siberian paleobasin. Also, the genus *Clathrodiction* appeared much earlier in other parts of the world (Fig. 358) than in Siberia, and that genus was probably not derived from *Stelodiction*, as shown in Figure 359, but its evolutionary pathway was probably in the opposite direction, from *Clathrodiction* to *Stelodiction*. In general, it is not easy to determine evolutionary patterns based only on one or two sets of regional data; a broader temporal and spatial approach is needed to achieve meaningful patterns of origins and dispersal worldwide.

In terms of the record of the earliest evolutionary relationships, KHROMYKH (2010, p. 687) has shown that the stromatoporoid *Priscastroma gemina*, with its two variants, *P. gemina* forma “A” and forma “B” (Fig. 359), comes from the upper Kochakan Formation, within the Mukteian horizon (or local stage) of the Moiero River basin section of the Siberian Platform, equating with the *Didymograptus murchisoni* graptolite Zone (within the middle-upper part of the Darriwilian stage). KHROMYKH (2010, p. 689) mentioned the possibility that the genus *Zondarella*, described previously from the early Mid-Ordovician (Dapingian) of Argentina (KELLER & FLÜGEL, 1996), might be ancestral to *Priscastroma*, but no evidence has emerged to indicate this taxon is present in critical Siberian sections; furthermore, it appears that the genus *Zondarella* has closer links to pulchraminidids than to stromatoporoids (see above, p. 578).

Of significance are the appearances of a number of other distinctive, short-lived taxa in the Mukteian stage of the Moiero River basin section. In addition to *Priscastroma*, such forms as tabulate coral *Cryptolichenaria* SOKOLOV, 1955 (see KANYGIN, MOSKALENKO,

& YADRENKINA, 1988, p. 5; KANYGIN, 2001, p. 610) occur. Apparently, according to KANYGIN (2001, p. 610), such forms first appeared on the eve of the great “ecologic revolution” (a radiation event), but they did not leave direct descendants, only variants like the ones associated with *P. gemina*. These were responsible for producing the two main, long-lived lines of labechiid descent involving *Cystostroma* and *Labechia* (this last genus appeared in the late Mid-Ordovician in the paleobasin but is not recorded in the Moiero River composite section—see KHROMYKH, 2010, p. 689, fig. 2). The associated major taxonomic diversification event involved a number of marine benthic groups (e.g., stromatoporoids, corals, bryozoans, brachiopods, trilobites, ostracodes, and others) early in the next regional stage (early Volginian; see KANYGIN, 2001, p. 609–610, fig. 3; KHROMYKH, 2010, fig. 2; and Fig. 359), at a level some 25 m above the initial appearance of *Priscastroma*, in the overlying Moiero Formation of the Moiero River basin section. *Cystostroma* (e.g., *C. insuetum* NESTOR, 1976) occurs at this level and equates with the *Hustedograptus teretiusculus* graptolite Zone (see correlation chart in KANYGIN, MOSKALENKO, & YADRENKINA, 1988), which is correlative globally with the uppermost part of the Darriwilian stage. This Siberian sequence between the Muktiean and Volginian is here inferred to be stratigraphically equivalent to the Chazyan interval in eastern North America, that is, between the Day Point and Crown Point formations (lower to middle Chazy Group), where GALLOWAY and ST. JEAN (1961) and KAPP and STEARN (1975) described the earliest North American labechiid species of *Pseudostyloclytion lamottense* (SEELY, 1904) and *Cystostroma vermontense* GALLOWAY & ST. JEAN, 1961.

On the other hand, KHROMYKH (1999b, p. 229) has erroneously suggested that the lower part of the Chazy Group (Day Point Formation) should be correlated with higher levels (middle of the Moiero Formation), based on OXLEY and KAY’s (1959, p. 825)

field identification of “masses of *Stromatocarium*” in the lower part of the Day Point Formation. Others have attempted to find this stromatoporoid in the Day Point Formation, without success. For example, PITCHER (1964, p. 648), in his detailed survey of Chazy reef assemblages, considered that most reports of *Stromatocarium* from the Day Point Formation probably referred to misidentified bryozoans. Clearly, the OXLEY and KAY determination has not been substantiated by the paleontological studies of Chazy stromatoporoids from Vermont and New York by GALLOWAY and ST. JEAN (1961) and KAPP and STEARN (1975). The genus *Stromatocarium* is instead characteristic of the disconformably overlying Black River Group (representing the upper part of the Sandbian stage) in the same region of eastern North America (GALLOWAY & ST. JEAN, 1955, 1961; HOFMANN, 1963, fig. 9; FISHER, 1968; KAPP & STEARN, 1975; BERGSTRÖM & others, 2009).

The major evolutionary event that occurred in shallow carbonate seas of different circumequatorial parts of the world during late Middle Ordovician (mid-late Darriwilian) time is represented by synchronous appearances of stromatoporoid-bearing Chazy reefs in eastern North America and the events and dramatic diversity changes recorded in mainly level bottom communities (including small stromatoporoid-bearing bioherms and biostromes) in the Siberian paleobasin (KANYGIN, 2001). Also, there were other stromatoporoid-bearing sequences in different parts of North America (Laurentia), and in Asian parts of northern China, Korea, and Malaysia (mainly parts of blocks associated with tropical East Gondwana) that contain genera of more or less the same mid-upper Darriwilian age (see Paleobiogeography of the Paleozoic Stromatoporoidea, p. 653–689).

The earliest appearances in Australia are in Tasmania and New South Wales, including records of *Labechia*, *Labechiella*, *Stratodicyon*, *Stromatocarium*, and ?*Aulacera*

(WEBBY, 1979a, 1991; PICKETT & PERCIVAL, 2001), correlating with a level close to, but just above, the Middle–Late Ordovician boundary (basal Sandbian Stage).

In addition, a marked, “sudden dominance of stromatoporoids,” was reported by HARPER, STOUGE, and CHRISTIANSEN (2004, p. 157; 2005, p. 49) from the lower Middle Ordovician succession of “inshore” aspect, within the upper Cape Weber Formation of Albert Heim Bjerge, northeastern Greenland. The radiation of so-called stromatoporoids apparently occurred in the Dapingian (=early White-rock) age, and this is much earlier than the confirmed major worldwide diversification of stromatoporoids (with its widespread appearances of earliest representatives of the order Labechiida) during mid- to late Darriwilian time (see previous discussion, p. 581–583; and see WEBBY, 2004b, p. 112–114). STOUGE and others (2002, p. 122) also recorded “stromatoporoid bioherms” from a stratigraphically higher part of the Albert Heim Bjerge sequence, within the upper part of the Heimbjerge Formation, of late Darriwilian (=late White-rock) age (see also SMITH & BJERRESKOV, 1994, p. 20 and chart 1). These preliminary field-based discoveries, especially the finds of so-called stromatoporoids from the Dapingian are of considerable interest, but none of the collected specimens has been subjected to rigorous, detailed study using thin sections (Svend STOUGE, personal communication, February 2007). Until such studies are undertaken by specialists, it will remain a matter for speculation whether the Dapingian takeover of so-called stromatoporoids is a localized, early radiation event restricted to Greenland, or whether the collected hypercalcified fauna proves to represent a variety of other skeletonized groups that are unrelated to indubitable stromatoporoids.

### LATE ORDOVICIAN ORIGINS OF CLATHRODICTYIDA

The order Clathrodictyida exhibited characteristic laminar skeletons (NESTOR, 1994) and initially appeared during the Late Ordo-

vician (early Katian). The genus *Ecclimadictyon* NESTOR, 1964a, with its zigzag laminae, was first to appear, and then *Clathrodictyon* NICHOLSON & MURIE, 1878, with its more gently inflected laminae, appeared a little later (WEBBY, 2004b). This was about 10 myr after the first appearances of labechiid stromatoporoids. The two genera became widely distributed through the latest Ordovician. Later, three additional genera, *?Plexodictyon* NESTOR, 1966a, *Camptodictyon* NESTOR, COPPER, & STOCK, 2010, and *Stelodictyon* BOGOYAVLENSKAYA, 1969a, appeared, but initially the first only maintained a distribution in New South Wales (NSW), the second, also in NSW and the Russian–Chinese Altai, and the third, in Estonia and Siberia. In terms of the origins of the clathrodictyids, NESTOR (1994) has shown them diverging from the labechiid family Rosenellidae, early in the Mid-Ordovician. But there is no evidence of such an early clathrodictyid fossil record, so it is much more likely that a much later divergence occurred, possibly from rosenellids in the Late Ordovician, close to the boundary between Sandbian and Katian stages (formerly mid-Caradoc). Otherwise, perhaps a basically clathrodictyid morphology could have been derived from a *Cystostroma*-like ancestor at this time. Some qualifications remain, however, when it comes to explaining exactly the steps required for a simple labechiid ancestor, with denticles that grew upward off cyst plates, to have evolved into an early clathrodictyid, where the short, commonly superposed pillars arose as downward inflections of successive laminae (WEBBY, 1986, p. 157). This event may have coincided with the interval of the greatest circumequatorial spread of Ordovician reefs (WEBBY, 2002), when many other groups of organisms (e.g., rugose corals, echinoderms, bryozoans, rhynchonelliformean brachiopods, and vertebrates) were attaining significant peaks of global diversity (WEBBY & others, 2004).

STEARNS (1980) and NESTOR (1994) maintained that the most characteristic families of the order Clathrodictyida were the families

Clathrodictyidae KÜHN, 1939b, featuring gently inflected laminae, and the Actinodictyidae KHALFINA & YAVORSKY, 1973 (formerly Ecclimadictyidae STEARN, 1980), exhibiting crumpled to chevron or zigzagged laminae. The Clathrodictyida are a major cosmopolitan group, and the two families show well-defined, parallel development through the Silurian and Devonian (NESTOR, 1997), but it is difficult to maintain a differentiation into two families in Late Ordovician, because the early records of *Clathrodictyon*, *Ecclimadictyon*, and ?*Plexodictyon* show a range of gradations between forms with regular and crumpled types of laminae (WEBBY, 1986, p. 156–157). There is more plasticity among these early clathrodictyids, and Silurian-based classification simply does not work as well for classifying the Late Ordovician forms.

The stratigraphic record from the initial Late Ordovician appearances of *Clathrodictyon* and *Ecclimadictyon* is more or less continuous into the Silurian, but the species diversification remained rather low across the Ordovician-Silurian boundary (NESTOR, COPPER, & STOCK, 2010, fig. 4), probably as a consequence of instability associated with the end-Ordovician glaciation (WEBBY, 2004b). However, the clathrodictyids were important contributors to reef growth during the initial warming phase of the late Hirnantian but did not diversify significantly through most of the earliest Silurian (Rhuddanian), until the significant radiation of clathrodictyids commenced in the mid-Llandovery (Aeronian) (NESTOR, 1997; NESTOR & STOCK, 2001). The most comprehensive classifications of the Clathrodictyida are presented by NESTOR (1997; NESTOR in STEARN & others, 1999), with subdivisions into five families of mainly Siluro-Devonian taxa, updated to six families with the addition of the new family Anostylostromatidae (see p. 766).

### LATE ORDOVICIAN ORIGINS OF ACTINOSTROMATIDA

One other stromatoporoid order may have had its origins in the Ordovician.

Three workers in particular, NESTOR (1960, 1964a, 1994), BOGOYAVLENSKAYA (1969a, 1974, 2001a), and STOCK (1983, 1994; STOCK in STEARN & others, 1999), have been active in establishing the origins, relationships, and classification of the actinostromatids. The genus *Plumatalinia* NESTOR, 1960, from the Late Ordovician (global late Katian = Pirgu stage of Baltoscandia) of Estonia, has been problematical because it shows morphological features that are typical of both labechiids and actinostromatids. NESTOR (1960, 1964a) initially assigned the genus to the Labechiidae. BOGOYAVLENSKAYA (1969b, p. 17, 25) subsequently recognized the Plumataliniidae (with sole genus *Plumatalinia*) as a new family of the order Labechiida, though she qualified her assignment to labechiids by noting that *Plumatalinia* could well be the ancestor of laminar stromatoporoids. Later she presented first a grouping in a stratigraphic chart, without specific discussion of the change showing the genus as ancestor of the order Actinostromatida and other descendants (BOGOYAVLENSKAYA, 1974, p. 22), then formally justified the transfer (BOGOYAVLENSKAYA, 1984, p. 70, 78, fig. 18) and has since maintained the family Plumataliniidae in order Actinostromatida (BOGOYAVLENSKAYA, 2001a). STOCK (1983, p. 168), on the other hand, treated *Plumatalinia* as a labechiid genus that probably gave rise to the Actinostromatida in the Late Ordovician or early Silurian, while NESTOR (1994, fig. 2) viewed the family Plumataliniidae as a Late Ordovician offshoot from the family Labechiidae (though he retained *Plumatalinia* in the order Labechiida). NESTOR also thought that the ancestral Late Ordovician plumataliniid line probably gave rise to all the descendant lines of Siluro-Devonian stromatoporoids belonging to the order Actinostromatida. He differentiated four families, the Actinostromatidae, Pseudolabechiidae, Densastromatidae, and Actinostromellidae.

STOCK (1994) supported BOGOYAVLENSKAYA's (1974, 1984) approach in transferring *Plumatalinia* from Labechiida, viewing

it as the likely ancestor of actinostromatids. He offered two different evolutionary schemes for the development of the group, each showing *Plumatalinia* as the Late Ordovician ancestor and well prior to the initial radiation into two or three main lines of descent in the Silurian. In the more traditional evolutionary scheme, the three lines of descent are represented by families Actinostromatidae, Pseudolabechiidae, and Actinostromellidae, and the ancestral *Plumatalinia* was incorporated in the Pseudolabechiidae. First appearances of the Silurian genera were the actinostromatid *Plectostroma* in the late Llandovery and the pseudolabechiid *Desmostroma* and densastromatid *Densastroma* at the beginning of the Wenlock. This was a somewhat different arrangement from the scheme proposed by NESTOR (1994). STOCK (in STEARN & others, 1999, p. 36) later proposed the downgrading of family Plumataliniidae to subfamily Plumataliniinae of the family Pseudolabechiidae BOGOYAVLENSKAYA, 1969b, but in this volume the subfamily names have been abandoned; hence, Plumataliniidae becomes a junior synonym of the Pseudolabechiidae.

In terms of the stratigraphic relationships, it is important to note that there is a gap in the continuity of the actinostromatid record, representing an interval of about 3.5–4 myr, between the restricted Estonian record of *Plumatalinia* in the Late Ordovician (late Katian = Pirgu stage) and the appearance of genus *Plectostroma* NESTOR, 1964a, in the late Rhuddanian (early Llandovery). This latter genus belongs to the family Actinostromatidae (not the family Pseudolabechiidae), so no direct lines of descent are preserved through this critical Hirnantian to early Rhuddanian interval of extinction and recovery impacts associated with the end-Ordovician glaciation (e.g., NESTOR & STOCK, 2001).

Heldur NESTOR (personal communication, November 2006) has since kindly supplied some additional details about the original Estonian material (its preservation and occurrences) used to found the

key taxon *Plumatalinia ferax*. A total of 15 specimens from 3 localities were used in the description of *P. ferax* presented in NESTOR (1964a). The material was collected from disused, overgrown farm quarries from the 19th and early 20th centuries. States of preservation vary considerably in the specimens studied and in some cases within a single specimen. The 3 states are represented by: (1) forms with long, low, flattened to wavy cysts (lacking longitudinal skeletal elements, as in simple labechiids), though they may show an incipient development of vertical canal-like interruptions; (2) forms with very fine, irregular skeletal meshwork between cyst plates and with columnlike structures in a few places; and (3) forms with a partially preserved fine microreticulate structure of columnlike structures and with a diffused outline. The microreticulate state is considered by NESTOR (personal communication, November, 2006) to be a primary structure, and therefore the resemblance is with microreticulate actinostromatids, though the particular microstructural type (acosmoreticular in *Plumatalinia*) differs from that found in other actinostromatid genera (*Densastroma* FLÜGEL, 1959, with orthoreticular and *Vikingia* BOGOYAVLENSKAYA, 1969a, with clinoreticular types; see STOCK in STEARN & others, 1999, and in Actinostromatida, p. 769–779).

WEBBY (1979a, p. 88; 1994, p. 375; WEBBY in STEARN & others, 1999, p. 13) originally considered that some of the fine subreticulate material may have been of secondary origin, pointing to similar features in other relatively poorly preserved labechiids, such as *Stratodictyon columnare* (WEBBY, 1969, pl. 118, 4–6). Examples of this microreticulate state are also developed in other labechiids, typically in the columns of *Pseudostylodictyon poshanense* OZAKI (see *Pseudostylodictyon*, Fig. 391a–b), and apparently also in *Pachystylostroma mammillatum* (see WEBBY, 1979c, fig. 3E–F). Consequently, it seems that *Plumatalinia* genuinely occupies an intermediate position between

labechiids like *Pseudostylocidictyon* and actinostromatids. It may indeed be a kind of missing link between the two groups, but some caution still needs to be exercised in claiming this relationship when such variability exists between the morphologies of the two groups.

A brief review of patterns of Silurian origins and relationships in other, nonlabechiid, stromatoporoid groups such as the stromatoporellids, stromatoporids, syringostromatids, and amphiporids is elsewhere (see section on diversity trends, p. 593–597).

# DIVERSITY TRENDS OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

## INTRODUCTION

Diversity trends in paleontology have been almost universally measured by counting taxa and plotting the number of families, genera, or species against time. The assumption of taxon counting is that the division into named units is a measure of the overall differences or disparity between sets of organisms. For stromatoporoids, no attempt has been made, nor is it being made here, to measure trends in what has been called disparity; that is, changes of morphology with time, as opposed to changes in taxa. Information and references to the literature on the differences between these two metrics can be found in such articles as FOOTE (1997), EBEL (2000), MILLER (2000), and NARDINE, ROUGET, and NEIGE (2005). The division of diversity found in organisms into discrete taxa is subjective (STEARNS, 1998), and this is a built-in weakness of taxon counting, but it can be minimized by using the taxonomy produced by a single paleontologist working with consistent principles, or a taxonomy agreed upon by a closely knit group of paleontologists working from common principles. Here, the latter approach is used, and the compilations of the four authors of the taxonomy of Paleozoic stromatoporoids (Colin W. STEARN, Barry D. WEBBY, Heldur NESTOR, & Carl W. STOCK; see Paleozoic Stromatoporoidea, p. 707; and Labechiida, p. 709–754) are the bases of this section (Fig. 360–361). Studies of diversity trends in the stromatoporoids have been published by NESTOR and STOCK (2001), COPPER (2002), WEBBY (2004b), and STOCK (2005). COPPER's (2002) diagram, which closely resembles Figure 360, was compiled from the review of stromatoporooid taxonomy by STEARN and others (1999). It

differs from the figure shown here in the lack of diversity fall-off at the Silurian-Devonian boundary, but COPPER's figures for diversity are roughly comparable to those used here. In each of these studies, the genus is the taxon counted, and this procedure is followed here.

In tabulating the generic diversity of a group in various time intervals, one can record only the time slices in which the genus has been found, or one can make the assumption that, if the genus is found in slices 1 and 4, it must also have existed in slices 2 and 3. The latter method is called the range-through method. The ranges of some labechiid stromatoporoids illustrate one of the problems with this method of tabulation. For example, the genera *Pachystylostroma* and *Labechiella*, which are likely to be progenitors of Famennian genera, have breaks in the continuity of their records; the former through Lochkovian to Givetian (about 31 myr) and the latter through the Llandovery to Wenlock (about 20 myr) (see Fig. 362). If the range-through method were used, it would exaggerate the diversity of labechiids in the Silurian system to some extent. For this reason, the range-through method is not used in this discussion, and the occurrence of a genus in a certain time slice has only been recognized when it has actually been recorded from rocks of the time interval.

Owing to divergences in opinion on taxonomic placement and on the age of certain collections, paleontologists do not agree on the precise generic diversity of stromatoporoids in the various time slices plotted in the figures. The figures on which the following discussion is based are attempts to reach consensus and are designed to show the relative rise and fall of diversity in stromatoporooid orders rather than the exact

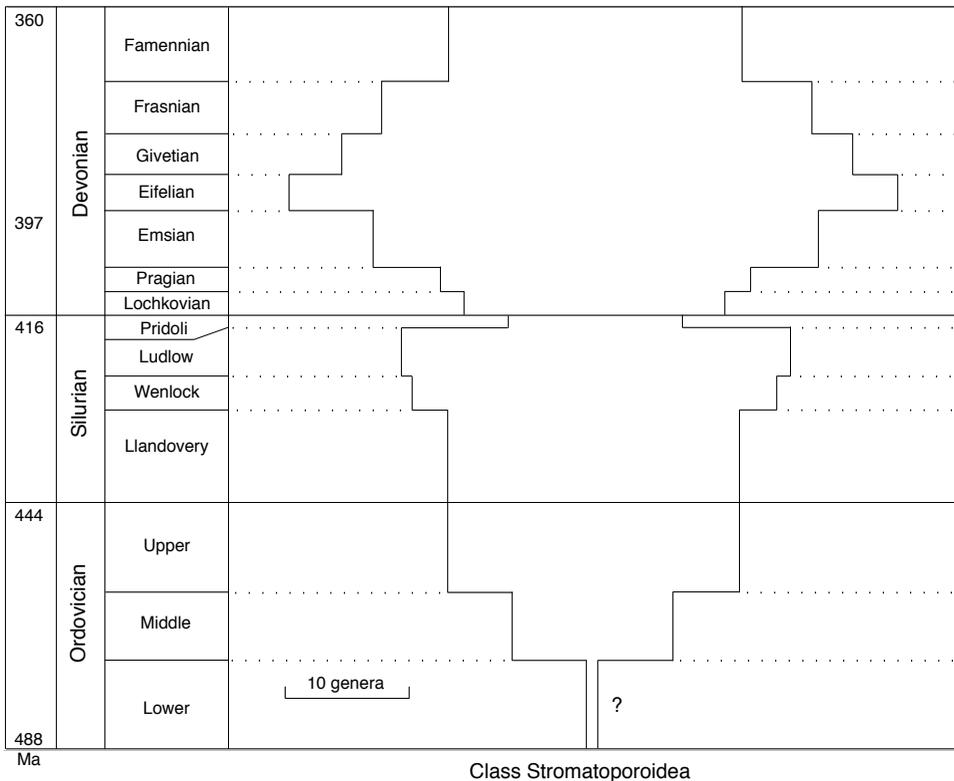


FIG. 360. Generic diversity of the class Stromatoporoidea. The vertical intervals are proportional to their time value in the geologic time scale according to GRADSTEIN, OGG, & SMITH (2004). Ages in millions of years (Ma) are indicated on the left; question mark in the Lower Ordovician denotes the author's view that the Pulchrilaminida is doubtfully ancestral to the class Stromatoporoidea. According to WEBBY (p. 575–592, p. 837–844), however, the new order Pulchrilaminida lacks close links to the Stromatoporoidea and, consequently, is best considered a completely independent hypercalcified sponge group of the class Uncertain. Note that in a more recent version of the time scale (COHEN & others, 2013), the base of the Ordovician is 485 Ma, base of the Silurian is 443 Ma, base of the Devonian is 419 Ma, base of the Middle Devonian is 393 Ma, and the top of the Devonian is 359 Ma (Stearn, 2010e).

number of genera in each time slice. The time scale used in calculations for Figure 360 is that published in 2004 by GRADSTEIN, OGG, and SMITH.

The causes for apparent changes in diversity in time have been widely discussed in the literature and are more fully discussed in the sections on evolution and extinction (see p. 575–592, and p. 599–612). Some of the factors affecting taxonomic diversity that have been recognized include: extent of exposure of rocks of various ages; extent of the seas depositing rocks of appropriate facies; number of paleontologists working on fossils of various ages; and all the environmental factors that affect the life history

of any group and particularly the rates of origination and extinction of taxa. The last points are of primary concern in the interpretation of the past; however, they are not the focus of this chapter, which describes the changes of diversity in time, rather than the causes of these changes.

## CLASS STROMATOPOROIDEA

The diversity of the stromatoporoidea, like that of many marine invertebrates, diminished at or near the close of the three geological periods in which they thrived. The downward trend at the end of the Ordovician is recorded only in the labechiids (Fig.

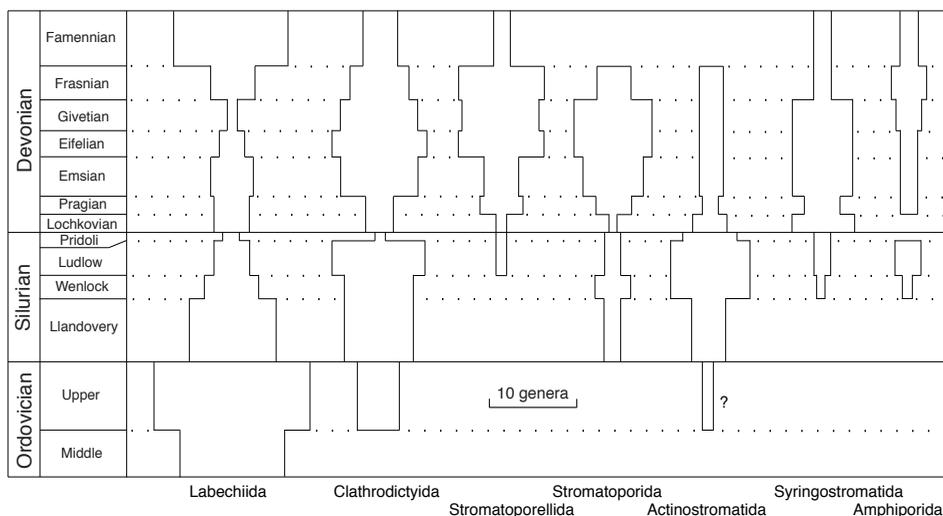


FIG. 361. Generic diversity of the orders of the class Stromatoporoidea, with the exception of the Pulchrilaminida. Time scale as in Figure 360. The extension of the Actinostromatida into the Upper Ordovician is based on the opinion of STOCK and NESTOR (personal communication, 2006) that the genus *Plumatalinia* is an actinostromatid, but WEBBY (see p. 590–592), on the basis of diagenetically altered skeletal material, believes the genus may be a poorly preserved labechiid, or that it occupies an intermediate position between the two groups (Stearn, 2010e).

361) and is compensated for by the rise of the clathrodictyids, stromatoporids, and actinostromatids. NESTOR and STOCK (2001) found that the crisis that abruptly affected other invertebrates at the end of the Ordovician is recorded by only gradual changes in the diversity of the stromatoporoids. From the Middle Ordovician until the end of the Ludlow, generic diversity of the order steadily increased (Fig. 360). The general decrease in diversity at the close of the Silurian reached its nadir in Pridoli time and was probably at least partially caused by the restriction of latest Silurian and earliest Devonian seas during this interval, leading to a consequent rarity of rocks of this age on the continental platforms. The extinction of the Paleozoic stromatoporoids at the close of the Devonian is fully discussed in the section on extinction patterns (see p. 599–612).

The greatest diversity of the class as a whole occurred in the middle of the periods (Fig. 360). In Ludlow and Wenlock times, diversity reached about 30 genera. The greatest diversity recorded in the compilation is 50 in Eifelian time, but values of

more than 30 genera were maintained until the late Frasnian crisis.

From the high level of diversity during the Eifelian, the class declined toward its extinction at the end of the Devonian. The crisis at the end of the Frasnian, which has been much discussed as the Kellwasser Event (see section on extinction patterns, p. 599–612) is a prominent step in the decline, but the expansion of the labechiids in the Famennian compensated for the marked effect of the crisis on three of the orders (Stromatoporellida, Stromatoporida, Actinostromatida, Fig. 361). The generic diversity of the nonlabechiid stromatoporoids fell from 30 in Frasnian time to 11 in Famennian time.

### LABECHIIDA

Both morphology and diversity history set the order apart from the rest of the stromatoporoids. Their origin is obscure, perhaps being with the enigmatic *Pulchrilamina* of the late Early Ordovician (Floian) of North America and *Zondarella* of the early Middle Ordovician of South America, separated by a gap representing about 4 million years from

the first labechiids (WEBBY, 2004b), although a problematical *Zondarella*-like taxon named *Ianilamina* PICKETT & ZHEN (in ZHEN & PICKETT, 2008), which was found recently in the early Darriwilian of New South Wales, arguably closes the gap to the first labechiid appearances. They suddenly appear as a diverse group (12 genera) in rocks of Darriwilian (late Mid-Ordovician) age in North America and southeastern Asia. Their diversity increases to almost 20 genera by the end of the Ordovician, when they began a long decline through the Silurian Period to a minimum of 2 genera in Pridoli time. Their latest Ordovician decline in diversity has been attributed to two sharp cooling to warming events of the Hirnantian glaciation (WEBBY, 2004b). During the Middle Devonian diversity peak of the other orders, the labechiids appear to have been restricted to Europe and western Asia, as they do not occur in the varied stromatoporoid faunas of the vast reef tracts of North America, South China (e.g., YANG & DONG, 1979), or Western Australia, although they do appear in the early Middle Devonian of eastern Australia (WEBBY & ZHEN, 1997). The sudden rise in diversity of the labechiids at the close of the Devonian (to about a dozen genera) is more fully discussed under the Kellwasser and Hangenberg extinction events that affected the whole class. Some feature of their adaptation allowed them to diversify, when the other orders were severely affected by the changes at the end of Frasnian time. However, they, like the other orders, could not survive events at the end of the Devonian Period, when the whole class became extinct.

### NONLABECHIID ORDERS

The Clathrodictyida appeared about 10 million years after the labechiids in the later half of the Late Ordovician, but they did not reach their diversity maximum until the Ludlow. Their first representative was the typically Silurian genus *Ecclimadictyon*, rather than the structurally simpler (and presumably

more primitive) genus, *Clathrodictyon*. The clathrodictyids are the most abundant and diverse stromatoporoids in middle Silurian reefs. They also thrived in the Middle Devonian, and about 11 genera are recorded from Eifelian rocks. The order was reduced slightly in diversity in Frasnian time and rendered almost extinct at its close.

The Stromatoporellida are largely a Devonian order and are represented in the Ludlow by the single aberrant genus *Simplexodictyon*, which seems unlikely to have been ancestral to the rest of the order. They probably arose from clathrodictyid stock. The diversity of the order shows a steady increase to a maximum of ten genera in Eifelian time, and this diversity was maintained until the late Frasnian crisis.

The Stromatoporida also reached their peak of diversity in the Devonian but are represented in the Silurian by several genera, beginning in the mid-Llandovery with *Lineastroma* and *Syringostromella*. Little change in the diversity of the order occurred until it began to increase in the Emsian. It reached its peak (nine genera) in the Givetian. The stromatoporoids collapsed in the late Frasnian crisis, and the order is only doubtfully known from Famennian rocks.

The first of the actinostromatids is thought to have been *Plumatalinia*, which appears to be transitional to this order from the labechiids and is plotted in Figure 361 in the Ordovician (see NESTOR, 1994, for discussion). The Actinostromatida reached their acme of diversity (about ten genera) during the middle of the Silurian period. Many of these genera had the closely spaced micropillars and microlaminae of the densastromatid family. Although the diversity of the actinostromatids decreased in the beginning of the Devonian, as the densastromatids died out or gave rise to the syringostromatids, the drop in diversity shown in Figure 361 misleads, if it is interpreted to imply the order was in decline in Devonian time, for the genus *Actinostroma* is abundant and ubiquitous in mid-Devonian carbonates. The generic diversity of the order remains at

about three from Emsian time to the crisis at the end of the Frasnian.

The Syringostromatida apparently arose from actinostromatid ancestors in the middle Silurian. A few Silurian genera have been assigned to the order, but they are largely a Devonian group. They maintained a diversity of about seven genera for most of the period but became rare in Frasnian rocks and did not survive into the Famennian.

The sticklike Amphiporida first appear in middle Silurian rocks and are represented as one or two genera in most time intervals of the Silurian and Devonian, until they became both diverse and overwhelmingly abundant in Frasnian carbonates. Recently (MISTIAEN, 1997), *Amphipora* has been found in Famennian rocks, but compared with its ubiquity and abundance in Frasnian rocks, it is there very rarely.



# EXTINCTION PATTERNS OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

## INTRODUCTION

The Paleozoic stromatoporoids were greatly reduced in abundance and diversity in the middle of the Late Devonian epoch and became extinct at its end, in events that have been described as mass extinctions, owing to the disappearance of many groups of marine animals at the same time. These intervals of high rates of declining diversity in the Devonian period are clearly shown by graphs of family diversity published by RAUP and SEPKOSKI (1982): between the Frasnian and Famennian stages (F/F) and at the Devonian-Carboniferous boundary (D/C). Unfortunately, they have been named after intervals of dark shales and limestones in the western German succession, as the Kellwasser and Hangenberg events, on the unproven assumption that the anoxic environments that the sediments represent were worldwide in extent. Evidence of ubiquitous anoxia at these times is equivocal at best, so the terms should be confined to local use. No attempt is made in this chapter to review the vast literature on mass extinction, but possible causes common to events in which the stromatoporoids declined, and to other extinction events in life history, are discussed.

What is a mass extinction and at what level are such events to be separated from background extinction (HOFFMAN, 1989)? Are the causes of mass extinction different from, or did they operate on a different scale from, the causes that throughout geological time have carried away the great majority of organisms that have ever lived? HOFFMAN (1989) thought that no extraordinary causes needed to be postulated to explain mass extinctions but rather the coincidence of causes that operate all the time.

NEWELL (1967) suggested that there were six major episodes of accelerated extinction in the fossil record and favored a mechanism of regression to explain them. Most later work on characterizing mass extinctions has focused on the manipulation of various editions of SEPKOSKI's compilations (RAUP & SEPKOSKI, 1982; SEPKOSKI, 1996 [unpublished but see BAMBACH, KNOLL, & WANG, 2004, p. 523]; SEPKOSKI, 2002) to assess extinction patterns of the so-called big five events: (1) end-Ordovician; (2) Frasnian/Famennian; (3) end-Permian; (4) end-Triassic; and (5) end-Cretaceous. WANG (2003), WANG and MARSHALL (2004), and BAMBACH, KNOLL, and WANG (2004) concluded that the evidence for accelerated extinction as a cause of these diversity drops could only be established for three of these (1, 3, 5) and that the proportional decline in generic diversity for 2 and 4 was included in a continuum of background extinction rates. The D/C (Hangenberg) event that marks the final demise of the Paleozoic stromatoporoids is not one of the big five and is marked by only a minor decrease in the proportional diversity curve. BAMBACH, KNOLL, and WANG (2004) accounted for two-thirds of the diversity drop at the F/F boundary by origination failure and attributed only the remaining one-third to increase in extinction rate. The search for causes of marked diversity drops and extinctions in the fossil record now becomes as much one for mechanisms of origination failure as for catastrophic extinction disasters.

Most of the studies of mass extinctions have been based on counting of taxa (families and genera), but other methods for assessing the magnitude of extinction events have been proposed. MCLAREN (1983) emphasized the extent of biomass loss as a measure

TABLE 30. Commonly recognized sequence of conodont zones in the Late Devonian–earliest Carboniferous succession and showing stratigraphic levels of F/F (Kellerwasser) and D/C (Hangenberg) extinction events (adapted from Sandberg, Morrow, & Ziegler, 2002).

Lower Carboniferous	⋮ <i>sulcata</i>
D/C	
Upper Devonian (Famennian)	<i>praesulcata</i> <i>expansa</i> <i>postera</i> <i>tachytera</i> <i>marginifera</i> <i>rhomboidea</i> <i>crepida</i> <i>triangularis</i>
F/F	
Upper Devonian (Frasnian)	<i>linguiformis</i> <i>rhenana</i> <i>jamieae</i> <i>hassi</i> <i>punctata</i> <i>transitans</i> ⋮

of the significance of mass extinctions. In particular, he drew attention to the demise of the Devonian reef facies in the F/F event. COPPER (1994) estimated that Frasnian reefs may have been ten times more extensive than modern ones and were reduced at the F/F event to insignificance. DROSER and others (2000) rated extinctions on the basis of four paleoecological levels, ranging from community-level changes to disappearances of whole ecosystems. They rated the changes at the F/F event as second, third, and fourth levels, but it is not clear how they would rate the D/C extinctions. MCGHEE and others (2004) rated the Late Devonian crises (which they considered together) as fourth in ecological severity of the big five and third in loss of marine familial diversity. They emphasized that the Late Devonian crisis was “. . . triggered in large part by a precipitous decline in speciation rates at the end of the Frasnian” (MCGHEE & others, 2004, p. 295).

Much of the discussion of the mid-Paleozoic extinctions involve reconstruc-

tions of the positions of the continents in Late Devonian time. Although many paleogeographic maps have been published, the disposition of the continents at this time is still in doubt. Many paleontologists have rejected the widely distributed maps of SCOTSE and MCKERROW (1990; and, for example, [www.scotese.com](http://www.scotese.com)) on the basis that both Siberia and Laurussia are too far north and Paleotethys too open. STREEL and others (2000) adopted the map by HECKEL and WITZKE (1979), because it accounts for the distribution of palynomorphs better. MCGHEE (1996) discussed the uncertainties of mid-Paleozoic paleogeography at length.

The early literature on the mid-Paleozoic extinctions has been summarized in books by MCGHEE (1996), HALLAM and WIGNALL (1997), and HALLAM (2004). KOEBERL and MACLEOD (2002) have recently compiled a series of papers on mass extinctions (Geological Society of America Special Paper 356). Another series of papers presented at the Geological Society of America’s symposium in 2003 was issued by OVER, MORROW, and WIGNALL (2005) and contains an important paper by STOCK (2005) on stromatoporoid originations and extinctions.

## PHYSICAL EVIDENCE OF LATE DEVONIAN CONDITIONS

### TIME SCALES AND BOUNDARIES

Certain hypotheses of Late Devonian extinctions depend on the coincidence, or lack of coincidence, of physical and biostratigraphic events. Unfortunately, the dates of these events are not known precisely, and they change as research progresses, making older theories invalid. The extinctions that decimated the stromatoporoids are commonly said to occur at the Frasnian-Famennian boundary and at the end of the Devonian period. But these extinctions do not define the boundaries, and proving they occurred at the boundaries is difficult. The boundaries are defined for the convenience of conodont workers at the beginnings of the

*triangularis* (F/F) and *sulcata* (D/C) zones respectively. The precise boundaries are set in the Montagne Noir sections in France at certain convenient beds (for the D/C a ferruginous crust) that correspond closely to the conodont distributions. The commonly recognized sequence of conodont zones in the Late Devonian succession that are used to position events in the subsequent discussion are listed in Table 30 (SANDBERG, MORROW, & ZIEGLER, 2002). In most sections, the abrupt F/F changes in fauna occur just above the last beds bearing the youngest Frasnian conodont fauna of the *linguiformis* zone. WALLISER (1996) suggested that the D/C boundary is actually about half a million years younger than the Hangenberg shales that have been said to mark it. The age in years of the two events can only be estimated by making assumptions about the length of the conodont zones and extrapolating from dated ash beds or lavas. Commonly accepted values are 364 Ma and 354 Ma (GRADSTEIN & OGG, 1996; MCGHEE, 1996; STREEL & others, 2000), but dates as divergent as 376 Ma and 362 Ma have been suggested. The International Commission on Stratigraphy time scale of 2013 places the base of the Famennian (F/F) at  $372.2 \pm 1.6$  Ma, and the base of the Carboniferous (D/C) at  $358.9 \pm 0.4$  Ma (COHEN & others, 2013). SELBY and CREASER (2005) place the D/C boundary at  $361 \pm 2.5$  Ma, on the basis of Re-Os dating of the Exshaw Shale.\*

#### STRATIGRAPHIC EVIDENCE

Great significance has been placed by Europeans on the occurrence at the F/F and D/C horizons of black shales and limestones

of the Kellwasser and Hangenberg formations. The Kellwasser dark shales actually are divided into two parts by some beds of limestone. Conodonts of the *linguiformis* zone (latest Frasnian) occur just below the Kellwasser interval. WALLISER (1996) has been particularly enthusiastic about a worldwide anoxia indicated by these black shales. However, this euxinic facies by no means universally interrupts the carbonate facies at the F/F horizon, and in western Canada and Australia, where the interval is extensively exposed, no anoxic interval interrupts the carbonate succession. In western Canada, dark, barren shales replace carbonates at the D/C horizon (Exshaw, Bakken, Chattanooga equivalents), but in much of eastern and arctic North America, long before the close of the Devonian period, the carbonate facies had given way to deltaic sandstones and siltstones. In the deltaic facies of the Upper Devonian there, black shales are so common that they are given no particular significance.

GELDSETZER, GOODFELLOW, and MCLAREN (1993) described the F/F contact on the Trout River in the Northwest Territories in detail. The beds below the contact are a stromatoporoid biostrome in the Kakisa Formation of *linguiformis* age. The contact is overlain by sandstone and is believed to represent an unconformity of lowermost *triangularis* age. In the southern Alberta Rockies (DAY & WHALEN, 2002), the F/F contact is underlain by stromatoporoid-bearing breccias in the Ronde Formation (of Kakisa age) and overlain by the Sassenach fine clastics (largely siltstones) in basal sections and on the shelf succession by the Palliser carbonates, whose basal beds appear to be of *crepida* age; i.e., the whole *triangularis* zone is missing on the shelf where the Sassenach is absent, owing to regression at this time. Apparently a regression at the F/F boundary caused withdrawal of the sea from the shelf area into the basins and was followed by a transgression in mid-Famennian time.

In the Canning Basin of western Australia, the F/F boundary is not marked by any

\*It may be helpful to explain the understanding accepted by the author of certain terms used to described events at the F/F and D/C boundaries. Boundary is an instant in time between the two ages substantially defined by the plane between the two stages at the stratotype section in the Montagne Noir; its position in other sections is approximated by methods of correlation. Horizon is the plane in the stratotype section that separates the two stages, and its position in other sections is established by correlation with the stratotype. Events are changes in environment that have occurred at or near the boundary between the ages. Where the boundary can not be determined precisely in a section that is not the stratotype, the term interval is used for the thickness of beds in which it is believed to be contained. Boundary extinctions are based on those fossils that range up to a specific level, but not above it.

conspicuous change in the stratigraphy that is indicative of transgression or regression (see COCKBAIN, 1989; BECKER & others, 1991). In southern China (WANG & others, 1991; MA & others, 2002), dark shales interrupt the carbonate successions in the *linguiformis* zone of the shallow-water facies but are not conspicuous in the marly deposits of deeper-water basinal sections. No equivalents of the Hangenburg facies occur in the D/C in southern China, and the boundary is within a bed of bioclastic limestone (HALLAM & WIGNALL, 1997). In Guilin (South China), karst features at the F/F boundary have been interpreted as evidence of regression (CHEN & TUCKER, 2004).

### ISOTOPE VARIATIONS

At intervals suspected of recording extraordinary faunal events (so-called bioevents), geochemists note excursions from baseline values of the isotopes  $^{13}\text{C}$  and  $^{18}\text{O}$ . The most extensive compilation of these values for the whole of Phanerozoic time was that of VEIZER and others (1999). Globally, average  $\delta^{13}\text{C}$  values are low during the Devonian, compared to higher values in the Silurian and Carboniferous. Values also climb steadily through the Paleozoic toward the Permian. Values of  $\delta^{18}\text{O}$  also dip (to about  $-2$ ) during the Devonian but climb toward  $+2$  in the Carboniferous near its end. SALTZMAN (2005) indicated only minor positive excursions of  $\delta^{13}\text{C}$  values at the F/F boundary and larger ones at the D/C boundary, to about  $+5$ .

Global compilations are too broad to provide much information on immediate causes of Late Devonian extinctions. Isotope studies of local sections and short time intervals should be more helpful. In the western German sections, the black shale intervals show positive excursions of  $\delta^{13}\text{C}$  (HALLAM & WIGNALL, 1997). JOACHIMSKI and BUGGISCH (2002) examined conodont apatite for changes in C and O isotopes and reported  $\delta^{13}\text{C}$  excursions of about  $+3\text{‰}$  at the F/F boundary. They recorded posi-

tive swings in both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  in late *rhenana* and early *triangularis* times. GELDSETZER, GOODFELLOW, and MCLAREN (1993) recorded zigzag excursions in both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  across the F/F boundary on the Trout River. WANG and others (1991) reported  $\delta^{13}\text{C}$  shifts from  $+1\text{‰}$  to  $-2.5\text{‰}$  at the southern China boundary and concluded that this indicates a reduction in surface water biomass. STREEL and others (2000) summarized the evidence of  $\delta^{13}\text{C}$  as equivocal at the F/F boundary, and HALLAM and WIGNALL (1997) indicated that there are no excursions of carbon isotopes at the D/C boundary.

### EVIDENCE OF IMPACTS

Evidence for the occurrence of asteroid or comet impacts at Late Devonian times of mass extinction comprises iridium anomalies, microtektites, impact breccia, and craters.

Two iridium anomalies have been recorded in the Late Devonian but have been dismissed as either being of insignificant magnitude to indicate a major event or as occurring at the wrong time. The first, at the F/F boundary in Guangxi, China (WANG & others, 1991) shows an Ir deflection of only about 0.21 ppbillion from that of adjacent strata. The second, at a bed rich in *Frutexitis* fossils in the Famennian of Western Australia, is generally considered to be caused by organic concentration of platinum group elements, rather than by an impact, and is not at either the F/F or D/C horizons.

Microtektites, the small globules of fused rock that have been considered indicative of impact events, have been found at the F/F boundary in Europe (at Hony, Belgium; CLAEYS & others, 1996) and South China, but, as WALLISER (1996) pointed out, these indicators are not uncommon in the insoluble residues extracted for conodont analyses throughout the Paleozoic. Since extraterrestrial matter of various calibers is continually raining through the atmosphere, the presence of some microtektites at any particular

horizon is not, in itself, good evidence of a catastrophic event.

Craters and breccias provide more direct evidence of bolide impact. MCGHEE (1996, 2001) has proposed that the Siljan Crater in Sweden, the Flynn Crater in Tennessee, and the Alamo Crater and breccia in Nevada are evidence that impactors were the ultimate cause of the F/F extinctions. Although the Siljan, the largest of these craters at 52 km in diameter, was at one time thought to correspond in time to the F/F event, changes in the time scale have since placed all the craters at approximately the time of the *punctata* zone, which is about 3 million years before the close of the Frasnian. To account for the time difference, MCGHEE (2001) applied a lag-time multiple impacts hypothesis to explain how these bolides could have been the ultimate cause of environmental changes that brought about the extinctions. TAPANILA and EKDALE (2004) reported that stromatoporoids overlie the breccia deposits from the Alamo event, and apparently the impact had no lasting effect on the stromatoporoid community. By 2006, MCGHEE recognized that all known impact events appeared to predate the F/F boundary, if the date of 376 Ma that he accepted was valid. However, recent studies of the Siljan crater using laser-argon dating (REIMOLD & others, 2005) give a date of  $377 \pm 2$  Ma, which is outside the error limits of the 2013 date for F/F of the International Commission on Stratigraphy ( $372.2 \pm 1.6$  Ma). Hypotheses linking impacts and extinction are frequently modified as different dates for the events continue to be revised.

There is no sure evidence of an impact or volcanic event associated with the D/C boundary; however, estimates of the times of impacts of the Charlevoix crater in Canada ( $357 \pm 15$  Ma) and the Woodleigh crater in Australia ( $359 \pm 4$  Ma) are within the range of estimates of the D/C boundary on the International Stratigraphic Commission Scale ( $359 \pm 2.5$  Ma) (MCGHEE, 2006).

The Woodleigh structure in the Carnarvon Basin of western Australia has been proposed

as evidence of a Late Devonian impactor large enough to form a crater 120 km across (MORY & others, 2000). The size, nature, and date of this structure is controversial, and discussions and replies can be followed through papers in Earth and Planetary Science Letters (for example, REIMOLD & KOEBERL, 2000; RENNE & others, 2002).

### EVIDENCE OF GLACIATION

Traces of glaciation near the paleopoles have been recognized generally as evidence of worldwide cooling. Considerable discussion of the age of glacial deposits and glaciated surfaces in Brazil and North Africa has been summarized by STREEL and others (2000). Although they postulated cooling as a cause of the F/F extinction event, there is no evidence of glaciation at that time. However, evidences of miospore distribution, diamictites, and glaciated surfaces of latest Famennian age (D/C) are cited by STREEL and others (2000) as clear evidence of glaciation near the southern polar regions, close to Brazil and North Africa.

FISCHER (1984) pointed out that important climatic changes were taking place near the close of Devonian time when he defined his supercycles. The change from Earth's greenhouse condition to the icehouse condition, the end of the warm seas and extensive reefs of the early and middle Paleozoic, and the beginning of widespread and prolonged glaciation in the southern hemisphere took place in the Famennian but must have been relatively gradual.

### LATE DEVONIAN DECLINE OF STROMATOPOROID DIVERSITY

Not all investigators agree that the Paleozoic stromatoporoids became extinct at the end of the Devonian period. MISTIAEN (1984b, 1994) has proposed that, with the changing ocean environments of the Sandberg Supercycle, the stromatoporoids merely lost the ability to secrete a carbonate skeleton until they reappeared as the Mesozoic

TABLE 31. Species and generic diversity of stromatoporoids (new).

Area	Author and date	Givetian			Frasnian			Famennian		
		sp.	gen.	s/g	sp.	gen.	s/g	sp.	gen.	s/g
Afghanistan	Mistiaen, 1985	34	19	1.8	18	10	1.8	3	3	1.0
Belgium	Lecompte, 1951 in 1951–1952*	56	11	5.1	61	11	5.5	4	3	1.3
Poland	Kaźmierczak, 1971	32	12	2.7	19	12	1.6	–	–	–
Czech Republic	Zukalova, 1971 <sup>§</sup>	16	8	2.0	56	17	3.3	8	7	1.1
Western Australia	Cockbain, 1984	–	–	–	25	12	2.1	2	2	1.0
Western Canada	Stearn <sup>+</sup>	24	16	1.5	37	20	1.9	5	5	1.0

\*Famennian data: Conil (1961); <sup>§</sup>Famennian data: Friakova and others (1985); + Stearn (2010f).

stromatoporoids. He suggested that the changing Late Devonian marine environment caused stromatoporoid skeletons to decrease in density during Famennian time and eventually to disappear at its end.

That stromatoporoids persisted into earliest Carboniferous time (Tournaisian) has also been reported. The stromatoporoids originally reported from the Tournaisian of China have since been reassigned to latest Famennian. SMITH (1932) described *Labechia carbonaria* from early Carboniferous beds in England, but SOKOLOV (1955, p. 111, pl. 90, see caption) considered the name to be preoccupied, interpreting it as a chaetetid, which he renamed as *L. smithi*. The cystose structure of labechiids is duplicated in many types of rugose and tabulate corals, and fragments of these can easily be mistaken for a labechiid stromatoporoid. At present, no post-Famennian stromatoporoids, in the sense of the term used here, are confirmed.

Most accounts of Late Devonian faunas describe the decline in diversity of not only the stromatoporoids but also of many other groups approaching the F/F crisis. STEARN (1982a) identified the peak of diversity of the stromatoporoids in Givetian reefs and outlined the decline in diversity through the Frasnian worldwide and in local sections (1982a, 1987). On a worldwide basis, STEARN (1987) recognized a Frasnian generic diversity of 37 and a late Famennian diversity of between 20 and 24 genera (see also Fig. 360–361).

The difference in taxonomic diversity between Givetian and Frasnian stromatopo-

roid faunas is not as obvious as between Frasnian and Famennian stromatoporoids, when monographic treatments of particular basins are tabulated. The number of species and genera in Givetian, Frasnian, and Famennian beds derived from various monographs (and therefore taxonomically consistent) for well-studied faunas within larger areas (i.e., not just local sections) is listed in Table 31.

Obviously, some paleontologists have different taxonomic philosophies and distinguish more morphologic variants as different species within genera; hence the wide variation shown in the ratio of species to genera (s/g) in Table 31. As a result, the number of genera appear to be the better measure of diversity for comparison between different studies. In most areas, the difference in generic diversity between Givetian and Frasnian faunas is insignificant. In Afghanistan, the taxonomic diversity decreases through the Devonian, but in the Czech Republic, it increases into the Frasnian. For the few areas where a comparison of Frasnian with Famennian faunas is possible, the drop in diversity from an average of about a dozen Frasnian genera to two or three in the Famennian is striking.

STOCK (2005) tabulated the diversity changes in seven Devonian successions from around the world and noted that in nearly all the sections, generic diversity fell during the Frasnian and into the Famennian. Origination and extinction of stromatoporoid genera were also tabulated from the taxonomic review of STEARN and others (1999). For the first four stages of the Devonian, originations exceeded extinctions, but from the Eifelian time to the end of the period,

the rate of origination steadily declined and the rate of extinction increased, reaching a maximum in the Frasnian. STOCK (2005) also plotted overall generic diversity by stage through the Devonian. Diversity reached a peak in Eifelian time and declined slightly through Givetian to Frasnian time, but the difference between Emsian and Frasnian diversity is less than 10%, or only three genera. Famennian diversity was only half the diversity in the Eifelian.

The question of whether the decrease in diversity of stromatoporoid genera in Late Devonian time could be owing to the Signor-Lipps effect (SIGNOR & LIPPS, 1982) should be assessed. This effect produces an apparent decline in diversity toward abrupt extinctions and is caused by the decreased likelihood of collecting rare and poorly preserved species of fossils at the ends of their ranges. The effect is minimal for fossils of abundant animals and those with skeletons that are likely to be preserved, such as the stromatoporoids. It has largely been adduced in the interpretation of ranges of fossils in local sections rather than in regional and global diversity studies extending over tens of millions of years, as for the stromatoporoids.

Early and middle Famennian stromatoporoid faunas are known from the Czech Republic, Australia, and western Canada. They are much reduced in diversity from late Frasnian fauna but contain such typically Frasnian genera as *Amphipora*, *Stachyodes*, *Stromatoporella*, *Syringostroma*, *Gerronostroma*, and *Stromatopora*. In Australia (COCKBAIN, 1984), Famennian rocks contain *Clathrocoilon* and *Stromatopora* (STEARNS, HALIM-DIHARDJA, & NISHIDA, 1987, suggested this is a *Trupetostroma*). By mid-Famennian time, stromatoporoids had recovered to the extent that they were building small reefs in the carbonates of western Alberta.

The most remarkable feature of the Famennian faunas in North America, Russia, Kazakhstan, Siberia, and southern China, however, is not the presence of survivors

of the F/F decline but the abundance and diversity of the order Labechiida. The typical genus of these faunas is *Stylostroma*, but the labechiid root stock branched into as many as 13 genera in southern China. If these Chinese genera are subtracted from the Famennian generic diversity total, the decrease in diversity at the F/F interval becomes 86%. The distribution of the labechiid and nonlabechiid communities in the late Famennian has been discussed in the sections dealing with paleobiogeography (Paleobiogeography of the Paleozoic Stromatoporoidea, p. 653–689). Assemblages of nonlabechiids only, labechiids only, and mixed assemblages are separated geographically in late Famennian (Strunian) rocks, and they first appear to be localized around the equatorial Paleotethys ocean. On the basis of this distribution, STEARN (1987) suggested that the labechiids became dominant in the Famennian because they were more tolerant of cool water.

The abundance and diversity of the labechiids in latest Famennian rocks is more remarkable because the family is rare in nearly all other Devonian stromatoporoid faunas. WEBBY and ZHEN (1997) have reviewed the scattered occurrences in Lower and Middle Devonian rocks (Mid-Devonian England, Queensland; Lower Devonian Urals, Queensland, northeastern Russia), but the major monographs on Givetian and Frasnian stromatoporoids contain no mention of labechiids. STEARN (1983a) did describe a *Labechia* sp. from rocks of Emsian age in the Canadian Arctic, but ST. JEAN (1986) has suggested that this may be a misidentification of a cystose structure in *Syringodictyon*. YAVORSKY (1957) has described five species of *Labechia* from beds he identified as being of Frasnian age, southern Urals, and, if these beds are confirmed in age, they are a unique assemblage.

In summary, stromatoporoid diversity declined slightly from Eifelian time toward an ecological crisis at the end of the Frasnian stage; then the widespread reef facies of Frasnian time was greatly restricted and many genera became extinct. This drop

was the result of a major decline in rate of origination since the middle of the Devonian Period and a less significant increase in the rate of extinction. During latest Devonian time, a few surviving Frasnian genera accompanied a resurgent labechiid order to form small reefs scattered in most of the continental blocks until the end of Famennian time. The remaining stromatoporoid stock went extinct at the D/C boundary. The F/F boundary marks an important ecological change, and the D/C boundary an important taxonomic one.

### RESPONSE OF OTHER TAXA TO LATE DEVONIAN EVENTS

In assessing the nature of the environmental changes that determined faunal changes during F/F and D/C times, a survey of the changes in other taxonomic groups is useful. The numerous papers on the radical changes at the F/F boundary seem to have overshadowed and depreciated the changes that took place at the D/C boundary. Shallow-water faunas were not as much affected at the D/C boundary, but goniatites and hemipelagic ostracodes lost much of their diversity (WALLISER, 1996).

Summaries of the groups affected by both episodes can be found in the works of BUGGISCH (1991), WALLISER (1996), MCGHEE (1996), HALLAM and WIGNALL (1997), and HALLAM (2004), and these are not repeatedly cited in the following discussion. MCGHEE (1996) estimated that 14%–30% of families, 50%–60% of genera, and 70%–80% of species became extinct in the Late Devonian mass extinctions, between late *rhenana* and middle *triangularis* zones (i.e., the Kellwasser interval). MCGHEE and others (2004) place familial diversity loss of marine faunas at 21%.

The calcareous Foraminifera were in their initial interval of radiation in Givetian and Frasnian times, and their shells are common in Frasnian grainstones. They suffered a rapid decline at the F/F boundary from 30 to 2 genera. MCGHEE (1996) made much of the abundance of hexactinellid

sponges in the Devonian shelf sediments of New York as evidence of invasion of deep cool-water taxa, but this occurrence is very local, perhaps unique, and can hardly have worldwide significance. SORAUF and PEDDER (1986) considered the fate of the abundant Frasnian rugosans at the F/F boundary. They recorded that only 5 of the 47 genera of late Frasnian rugose corals survived into the Famennian. There is some evidence that deeper-water genera survived to radiate into shallow environments. Whether D/C events had a significant effect on rugosans is controversial. Tabulate corals were in decline in the Late Devonian and represented largely by branching forms such as *Thamnopora*. They were greatly reduced by the F/F change but little affected at the D/C boundary.

Bivalves and bryozoans both seem to have been little affected by either of the Late Devonian crises.

Cricoconarids had a precipitous decline at the F/F boundary, reducing from 6 genera to 1 genus. As they are generally regarded as pelagic in habitat and commonly preserved in dark shales, their decline is difficult to relate to some hypotheses of changing sea levels and rising anoxia. Ammonoids seem to have been facing crises throughout their history. As a result, investigators attach little significance to the fact that they declined in Frasnian time and recovered in the Famennian. However, about 85% of the goniatites became extinct at the end of the Devonian. FEIST (1991) documented the general decline of the trilobites in the Frasnian from a high of diversity in the Eifelian. Very few new trilobite genera were added in Frasnian time, and the trilobites were never again a significant part of shallow-water faunas in late Paleozoic time.

Brachiopods have been regarded as holding the key to climate change at this time, owing to the work of COPPER (1977, 1994) on South American faunas. The diversity of Frasnian brachiopods declined toward the F/F boundary; the number of genera reduced from 92 in the Frasnian to 23 in the Famennian. Thirty of the 33 families lost at

this point were tropical forms. The orders Pentameroidea and Atrypoida became extinct in Frasnian time (the latter in early *linguiformis* time). Orthids and strophomenids were greatly affected, but spiriferids and rhynchonellids were not. STIGALL RODE (in STIGALL RODE & LIEBERMAN, 2006) has studied changes in the brachiopod community at the Devonian biodiversity crisis using environmental niche modelling.

STREEL and others (2000) documented miospores. Their diversity shows a peak in the Givetian of about 58 species and a decline from Frasnian to Famennian from 51 to 23 species. Plant macrofossil diversity shows a similar decline. Chitinozoans survived the F/F boundary but, after a long decline, became extinct at the D/C boundary. Acritarch diversity collapsed at the end of the Devonian rather than at the F/F horizon. Ostracode history gives no clear signal, and their distribution and decline has been interpreted in various ways.

In summary, most fossil groups responded to Late Devonian environmental change by decreasing in diversity; most survived the two (or more) crises, but the stromatoporoidea did not. The extinctions, largely at the family and lower taxonomic levels, extended over a considerable period of time; MCGHEE (2001) suggested from late *rhenana* to mid-*triangularis* times.

### CAUSES OF LATE DEVONIAN EXTINCTIONS

Paleontologists have suggested many causes to explain mass extinctions. MCLAREN (1983) suggested that we should recognize a hierarchy of causes leading us to some ultimate cause; that is, if anoxia is the immediate cause of the extinction of shallow-water faunas, was the anoxia caused by transgression, was the transgression caused by ice-cap melting, was the melting caused by climate change, and was the warming caused by an increase in CO<sub>2</sub> in the atmosphere? The problems of identifying causes and distinguishing them from triggers in the interpretation of the stratigraphic record

has been examined by CLELAND (2001) and commented on by KILTY (2002) and BAILEY (2002). BAILEY (2002, p. 953) concluded that in stratigraphic interpretation: "The attempt to establish causality within reasonable doubt is for the most part futile and when attempted likely to be misleading." Earth systems are so complex and inter-related that retracing the whole chain of causation for events of hundreds of millions of years ago seems impossible, and we should be cautious of simplistic solutions.

In the search for causes of mass extinctions, the most powerful tool is selectivity: the difference in ecologic requirements between the organisms becoming extinct and those surviving. For example, if species that lived in the tropics become extinct, while cool-water species survive and occupy formerly tropical environments, then cooling temperatures are almost certainly part of the complex of causes.

Although many discrete causes of Late Devonian diversity decline have been suggested, they can be grouped into three general hypotheses: (1) extraterrestrial influences, impactors, or cosmic rays; (2) sea level changes and accompanying anoxia; (3) climate change, notably cooling, shown by and giving rise to Southern Hemisphere glaciation.

### BOLIDE IMPACT HYPOTHESES

Extraterrestrial matter continually impacts the atmosphere, and larger particles rain down on the Earth's surface. The evidence for this is usually widely distributed in marine sediments and is unlikely to have significant effect on marine life. The search for extraterrestrial causes, or triggers, for mass extinction is a search for anomalies in the rate at which this evidence is introduced into the marine record. The extent of the anomaly required for an extensive extinction has not been clearly defined but is usually stated in terms of the diameter of the impactor; i.e., a 10 km impactor should do the job. The question of how many

microtektites, or shocked quartz grains, demand our attention as causes or triggers, goes unanswered. The search for these signatures of impact at the F/F and D/C has yielded little evidence and that which has been adduced has been efficiently refuted (HALLAM, 2004, p. 76).

The evidence for bolide impact has been reviewed above and, apart from the occurrence of breccias, is not compelling. Coincidence of impact date of major sites with biostratigraphic events is difficult to establish. MCGHEE (2001) suggested that multiple impacts in early to middle Frasnian time (approximately *transitans* zone) would have produced an anomalous warm period in the general cooling trend of Late Devonian time associated with the transition from greenhouse to icehouse conditions. He proposed that the immediate cause of F/F extinctions was the abrupt return to the general cooling of oceans as the anomalously high CO<sub>2</sub> concentrations caused by the impacts was absorbed in the rapidly spreading plant community. Application of the multiple impact hypothesis to Late Devonian extinctions seems to be a final attempt to rescue the bolide hypothesis from rejection.

Suggestions that radiation from space may have caused mass extinctions can be traced back to SCHINDEWOLF (1954), who suggested that cosmic rays from a supernova explosion caused the end-Permian extinction. A similar hypothesis has been proposed more recently by Adrian MELOTT (see HECHT, 2003) that gamma rays from an exploding star caused the Late Ordovician event. SHAVIV and VEIZER (2003) have drawn attention to the probable effect of cosmic ray flux as a determinant of Phanerozoic climate but do not apply their model to extinction causes.

### ANOXIA, TRANSGRESSION, AND REGRESSION

The coincidence of the Kellwasser and Hangenburg intervals of dark shales and limestones with the extinctions in Europe has convinced many geologists there that

the spread of anoxia over continental shelves through transgression was an immediate cause of the biota changes. A corollary hypothesis is that the mid-Paleozoic oceans were chronically unventilated at depth, and it was this anoxic water spreading over the carbonate shelves that poisoned so many animals adapted to shallow, oxygenated waters (such as stromatoporoids). The hypothesis is also connected to the burial of large quantities of organic carbon in these dark shales and consequent draw-down of atmospheric CO<sub>2</sub> and decrease in temperature. JOACHIMSKI and BUGGISCH (2002) attributed positive excursions in δ<sup>13</sup>C as evidence of 20%–30% increase in burial of organic carbon in the ocean and hence a drawdown of atmospheric CO<sub>2</sub>. MURPHY, SAGEMAN, and HOLLANDER (2006), who studied two black shale intervals in the Devonian of New York that they correlated with the Lower and Upper Kellwasser horizons, recorded in them a positive δ<sup>13</sup>C excursion of 4‰ to 5‰. On the basis of this and changes in the C:N:P ratio of buried organic matter, they postulated that eutrophication of the water column was important in causing extinctions. BRATTON, BERRY, and MORROW (1999) studied the geochemistry of an anoxic interval in the Great Basin of the southwestern United States and concluded that it marked neither the end of the Frasnian nor the *linguiformis* zone, but ended about 0.1 million years before the F/F boundary. The interpretation of the positive shift in δ<sup>13</sup>C at the F/F boundary in some sections has been difficult to explain. ERWIN (2006) discussed various alternatives for similar changes at the end-Permian extinction.

MCGHEE (1996) pointed out that intervals of dark, organic-rich shales, much like the Hangenburg and Kellwasser, are common at many levels within the Late Devonian successions around the world, and the great majority have not been associated with extinctions or radical faunal changes. In addition, local anoxia is easy to accept, but worldwide oceanic anoxia is more difficult to model.

If the incursions of anoxic water onto shelves is taken as evidence of rise of sea level, then sea level must have fallen rapidly thereafter to account for the widely recognized regression at the beginning of Famennian time (STREEL & others, 2000; JOACHIMSKI & BUGGISCH, 2002; STOCK, 2005). In western Canada, for example, the F/F boundary appears to be associated with a disconformity formed by widespread regression from the carbonate shelf environments. Such regression would have restricted shallow-water habitats and might have led to increased competition between shallow-water benthic organisms and thus extinctions. BUGGISCH (1991) has constructed a complex cyclic model of rising and falling sea levels and anoxic shelves to explain the upper and lower Kellwasser intervals. His sequence can be summarized as follows: transgression → anoxia on shelves → organic carbon sequestering → decrease in atmospheric CO<sub>2</sub> → icehouse → glaciation → regression → erosion of organic C → increase in atmospheric CO<sub>2</sub> → greenhouse → increased organic production → transgression, and so on. MAY (1997) postulated that the Kellwasser and five other previous Devonian bioevents were all caused by rapid transgression of anoxic waters over the shelves. RACKI (1998) reminded us that rapid sea level changes can also be caused by tectonic events such as rifting, but commonly the postulated sea level changes are attributed to Late Devonian glaciation.

STOCK (2005) attributed the fall in diversity of stromatoporoid faunas in Frasnian time to the transgression of the Transcontinental Arch in North America and consequent mixing of faunas from the Eastern Americas realm and Old World realms. Whether the arch was an effective barrier to stromatoporoids from Eifelian to late Frasnian time, or if its flooding had more than a local effect on world faunas, remains to be proven.

HALLAM (HALLAM & WIGNALL, 1997; HALLAM, 2004) strongly supported anoxia as a cause of mass extinctions. He postulated

that a late Frasnian regression was followed by a Famennian transgression flooding the continents with anoxic waters that until then had been confined to the deep oceans.

In a similar hypothesis, KUMP, PAVLOVA, and ARTHUR (2005) suggested that during intervals of oceanic anoxia, the chemocline separating sulfidic deep waters from oxygenated surface waters could have risen to the surface, killing much marine life and introducing lethal doses of H<sub>2</sub>S into the atmosphere in Late Devonian time. Another hypothesis advanced by BAMBACH, KNOLL, and SEPKOSKI (2002) postulated that large quantities of CO<sub>2</sub> introduced into the atmosphere from an anoxic ocean's depths would more seriously affect invertebrates of lower metabolism and activity (such as stromatoporoids) than those with higher metabolic rates and would lead to less successful survival of such an event. The release of methane (CH<sub>4</sub>) from hydrates in the deep continental shelves by fall of sea level or rise of temperature has been proposed to account for the positive excursions of δ<sup>13</sup>C at extinction boundaries (ERWIN, 1993, 2006) and deleterious effects on the environment by increasing the greenhouse effect.

In conclusion, oscillations of sea level in Late Devonian time have certainly been documented, but their effects as controls on diversity and extinction are not obvious.

## GLACIATION IN THE SOUTHERN HEMISPHERE

When rapid transgressions and regressions occur in the geological record, stratigraphers turn to the growth and melting of continental ice sheets for explanation. The spread of ice beginning in mid-Carboniferous time over much of the southern hemisphere in the icehouse phase of the late Paleozoic has been accepted since early in the 20th century, but the identification of Late Devonian glaciation has been controversial. The evidence of diamictites and striated surfaces in northeastern Brazil dated palynologically has recently been reviewed by STREEL and

others (2000). They concluded that glaciation there, and possibly in North Africa, is well supported by stratigraphic evidence in the D/C interval but not at the end of the Frasnian. Still, to justify the extinctions in the F/F interval, they postulated a short glacial interval within a generally warm climate. The general cause of the cooling that brought on the glaciations is so-called sinking of the greenhouse gas CO<sub>2</sub>, in both marine organisms and rapidly spreading land vegetation. STREEL and others (2000) pointed out that, at present, the productivity in plant-matter mass on land is three times that of the sea, but this does not mean that it was so in Devonian time.

### GLOBAL COOLING

The fractionation of oxygen isotopes is dependent on temperature, and excursions in  $\delta^{18}\text{O}$  have been used as a proxy for temperature. GONG and XU (2003) warned, however, that  $^{18}\text{O}$  excursions can also be caused by changes in sea-water salinity. Temperature has also been used as a proxy for the extent of continental ice sheets, and the extent of ice has been used as a proxy for sea level. For example, STREEL and others (2000) suggested that the  $\delta^{18}\text{O}$  positive excursions at the F/F horizon can be correlated with a drop of sea level of 180 m, owing to the trapping of water in polar ice. In contrast, JOACHIMSKI and BUGGISCH (2002) suggested that  $\delta^{18}\text{O}$  values of  $-1\text{‰}$  indicate warm sea temperatures of about 26° C at this time. For comparison, recall that the steady decrease of water temperatures from Eocene time to the present leading to the Ice Age is represented by a  $\delta^{18}\text{O}$  from about 0‰ to +4‰. VEIZER and others (1999) correlated a positive swing of  $^{18}\text{O}$  with Late Ordovician glaciation and suggest that the rise in the Late Devonian may be correlated with a similar phenomenon at that time. The extensive  $\delta^{18}\text{O}$  determinations on mid-Paleozoic brachiopods published by BRAND (1989b) gave unrealistic seawater temperatures in the 36° C to 54° C range, which have been largely dismissed by later investigators as being influenced by diagenesis of his samples.

On the basis of oxygen isotopes from conodonts, JOACHIMSKI and BUGGISCH (2002) denied evidence of extensive Late Devonian ice sheets. The ocean temperatures for late Frasnian time derived from  $\delta^{18}\text{O}$  values of  $-1\text{‰}$  are warm, about 32° C; the two excursions in the oxygen isotope curves near the F/F horizon indicate temperatures falling to about 26° C. This decrease in temperature is comparable to that which accompanied the Pleistocene glaciation (4–8° C). However, they attributed the Late Devonian extinctions to general and episodic cooling and ultimately to the burial of organic carbon in so-called sinks and decrease in atmospheric CO<sub>2</sub>. JOACHIMSKI, VON BITTER, and BUGGISCH (2006) discussed the significance of  $\delta^{18}\text{O}$  to sea level changes in the Pennsylvanian cyclothems and suggested that a change of +1.7‰ would be equivalent to a temperature decrease of 7° C, if explained solely by temperature, and could have resulted in sea level falls of more than the 120 m experienced during Pleistocene glaciations.

The hypothesis that global cooling was one of the main causes of Late Devonian extinctions, which was first clearly stated by COPPER (1986), has been supported since by more and more evidence. COPPER's conclusions grew out of studies of South American brachiopods (1977). These cold-water faunas displaced the tropical brachiopods in Late Devonian time, clearly signalling a cooling event. Originally, COPPER (1986) suggested that the cooling was caused by the movement of the continents and closing of the Frasnian equatorial ocean (Paleotethys). Later, COPPER (1994) suggested that reefs and calcareous plankton have a great capacity to sink CO<sub>2</sub> and cause climatic change.

That global cooling, CO<sub>2</sub> in the atmosphere, sea level changes, and even glaciation are connected with the burial of organic carbon at the beginning of the Icehouse Earth is a common thread in many recent hypotheses. The increase in removal of C<sub>org</sub> from recycling to the atmosphere, as

evidenced by organic-rich sediments and positive  $\delta^{13}\text{C}$  excursions, is most commonly attributed to the spread of plants upon the land (ALGEO & SHECKLER, 1998) but may also have been related to ocean anoxia, slowing the decay of marine organic matter and sequestering it in black shales.

MCGHEE (2006) based his discussion of extinction hypotheses on a model of falling global temperatures, starting at the beginning of the Givetian and culminating in late Famennian glaciation. The ultimate cause of the cooling was falling atmospheric  $\text{CO}_2$  content, owing to the rise of vascular plants. MCGHEE postulated that this steady cooling trend was interrupted by a brief, sharply defined, warmer greenhouse interval in late Frasnian time, caused by impacts or volcanic phenomena (flood basalts), whose collapse led to F/F extinctions. The climatic changes could have been episodic to explain the series of pulses that MCGHEE identified in late Frasnian extinctions. Similar episodic extinction events have not been identified in the history of the stromatoporoids.

STEARNS (1987) suggested that general cooling of Late Devonian climates led first to widespread F/F decline in diversity and abundance of the stromatoporoids, the rise of the cool-water tolerant labechiids, and eventually to the demise of the whole class (D/C). COPPER (1994) has suggested that the greater effect of F/F events on the corals than on the stromatoporoids means that the former were more sensitive to environmental change than the latter.

CLARKE (1993) commented on the role of temperature alone in causing extinction of marine organisms. He emphasized changes in seasonality in interrupting reproductive cycles as being more important than changes in temperature. The latter are more likely to cause changes in the distribution of organisms than their extinction. He noted that humans, as warm-blooded animals, may see colder temperatures as detrimental, while many marine invertebrates thrive in frigid waters.

Not all models of Late Devonian temperatures postulate overall steady cooling of the atmosphere during this interval, and several postulate warm seas in Frasnian and Famennian time. Until a detailed temperature curve is agreed upon, hypotheses linking temperature and extinction will continue to be subject to modification. TWITCHETT (2006) has summarized studies of mass extinctions and concluded that climate change is the only reasonable explanation for most of these events.

## CONCLUSIONS

That changing conditions as the Devonian Period came to an end were challenging to shallow-water faunas is clearly evident; that they were catastrophic is harder to prove (HALLAM, 2004). The appeal of the so-called New Catastrophism has led many to seek an extraordinary event or events and a unique cause to explain the deteriorating marine environment of Late Devonian time. In consideration of GOULD's (1985, 1989) proposal that contingency and, in particular, randomly caused episodes of mass extinction are the fundamental controls on the history of life, paleontologists have concentrated on the study of these time intervals. Certainly, the attention given by media and public to the abrupt extinction of the dinosaurs coincident with an extraordinary astronomical event has focused attention on other similar incidents in life history and suggested similar abrupt scenarios. But there is no reason why each of the big five extinction events should have the same cause; on the contrary, marked differences in the stratigraphic record at the five boundaries suggest just the opposite. The evidence for each event must be weighed separately. For example, although the coincidence in time with extinction events at the end of the Cretaceous and Permian of extensive flood basalts in India and Siberia, respectively, has been suggested as a cause of the extinctions, no such extensive extrusions coincide with the Devonian extinctions. The

evidence for each extinction event in the geologic record must be weighed separately.

Extinctions at all hierarchical levels: orders, families, genera, and species, took place continuously throughout life history, as the changing environmental determinants became inhospitable to this or that organism. As the cycles of change in limiting environmental parameters such as (in the marine environment) temperature, salinity, oxygenation, nutrient level, depth, and illumination, took place, different organisms with different sensitivities to these parameters became extinct. When conditions adverse to marine life in a few of the parameters coincided in time, several groups became extinct; at those rare times when adverse conditions coincided in most of them, then what has been called a mass extinction occurred. If this is the case, then not only are such episodes inevitable at random times in the history of life, but they have no immediate single cause, only multiple causes. The model is further complicated by the intimate interrelationships of the ecological determinants, so that looking for a single trigger in this web of causes is frustrating. JABLONSKI (2000, and references therein) argued that large-scale ecologic systems (such as the mid-Paleozoic reef complexes) have an inherent resistance to perturbations and require an external extraordinary event to disrupt them. A hypothesis of multiple

coincident causes has also been discussed by ERWIN (1993, 2006).

All the major mechanisms of Late Devonian extinction that have been proposed have evidence in their favor and evidence against them. That we will ever be able to reconstruct the events of hundreds of millions of years ago seems unlikely. What seems likely is that some combination and interaction of climate change, anoxia, sea level variation, and sinking of carbon dioxide resulted in environmental instability beyond the capability of much of the warm-water marine benthos to accommodate. Whether extraterrestrial influences had any effect as a trigger remains to be proven. RACKI (2005) has summarized many of these arguments and provided an extensive bibliography.

Only a likely scenario can be postulated. Deteriorating marine conditions associated with temperature fall slowly affected the rate of origination of stromatoporoids from Givetian to Famennian time. The ultimate cause of such global climatic change is unlikely to be determined from paleontological or stratigraphical studies. This decline in originations was intensified into widespread extinctions in the F/F and D/C intervals by changes in sea level, causing habitat loss and locally catastrophic flooding of anoxic waters onto shelf environments. By the end of the Devonian, stromatoporoids were unable to withstand further stress and became extinct.

# BIOSTRATIGRAPHY OF THE PALEOZOIC STROMATOPOROIDEA

B. D. WEBBY, C. W. STEARN, and HELDUR NESTOR

## INTRODUCTION

Although all life forms have a limited existence in time, some are more valuable than others for recognizing a particular time interval. Such species have short stratigraphic ranges and wide distribution, and are, therefore, potentially useful in distinguishing short intervals of time. Also, for groups to be potentially valuable for dating, they must have been studied and understood taxonomically. In addition, students of groups of fossils that are valuable in biostratigraphy must be able to agree on a consistent taxonomy. The stromatoporoids only partly meet these requirements. Only within the past three decades has the broadening of the species concept allowed the recognition of species from one region to another. Previous research was concentrated on distinguishing new taxa by refining the differences between specimens, and the species established in one continent or country were rarely identified in other parts of the world. For example, STEARN (1979) compared monographic descriptions of Frasnian faunas from the Ardennes (Belgium), Poland, and the Czech Republic, and showed that the taxonomic principles used by the investigators to distinguish species led to the conclusion that none of the 132 species of stromatoporoids were common to all three areas, even though they are separated presently by only a few hundred kilometers in Europe.

Faunas that do not have common species cannot be correlated. Not until a broader species concept, and an appreciation of the degree of variation inherent in stromatoporoid species are accepted, can the true biostratigraphic potential of the group be

fully assessed. Yet, despite this realization, some stromatoporoid species and assemblages have been recognized as having wide distribution and short duration, and they therefore have considerable potential for zonation and correlation.

Stromatoporoids occur commonly in Ordovician, Silurian, and Devonian carbonate successions but have seldom been used primarily as biostratigraphic indicators. They occupied mainly warm, well-circulated, shallow, marine, carbonate shelves, especially the reef and shoal habitats of equatorially disposed continental platform and island-arc settings. In reef and shoal facies, stromatoporoids are often the only fossils available for biostratigraphic studies. Notwithstanding their prominence in many Paleozoic carbonate successions, they have remained comparatively poorly understood. Taxonomic approaches have long been founded on differentiating a species on the basis of a single, or a few specimens, rather than evaluating the variation that existed among many individuals of a particular species. In addition, some taxonomists have used traits (such as astrophorae, e.g., BOGOYAVLENSKAYA, 1965b, and subsequently) for essential specific characters and for guides to phylogeny and classification, which are regarded as trivial by other research workers, making their taxa difficult to recognize in other parts of the world.

The basic framework of a modern-type of stromatoporoid taxonomy was presented by NICHOLSON (1886a, p. 2) some 120 years ago. He stressed the necessity for investigation of diagenetic alteration across a large number of specimens and assessment of the range of variability in populations of the

species with use of adequate numbers of collected samples. However, NICHOLSON's approaches were not adopted by many stromatoporoid workers, at least not until the last few decades. Too many workers have been intent on multiplying the numbers of species based on differences between a few, often fragmentary specimens. A more rigorous approach is required for sampling and studying a stromatoporoid species. This entails using a larger number of specimens as the basis for fully describing the range of diagnostic morphological features: the variability of form and attributes of the species that arose from diagenetic alteration.

Three promising approaches to biostratigraphic correlation using Ordovician–Devonian stromatoporoids are the following.

1. Compilation of range charts (both at genus and species levels).
2. Establishment of sets of laterally adjacent successions of species-based zonal assemblages (NESTOR, 1982, 1990b, 1999b).
3. Development of a succession of species-based zonal assemblages tied to the zonation of conodonts (STEARNS, 1997a, 2001).

Continuity of rigorous taxonomic work through the Ordovician to the Devonian stratigraphic record is needed to provide the basis for more precise biostratigraphic analyses, using one or more of the above-mentioned approaches, hopefully leading to recognition of many more diagnostic, zonally restricted, but widely distributed stromatoporoid species. Each of the three biostratigraphic approaches is further discussed below.

### RANGE CHARTS

KÜHN (1939b, p. 14–15) assembled one of the earliest broad-scale compilations of the stratigraphic distribution of important stromatoporoid genera. Another, more comprehensive, tabular representation of Paleozoic and Mesozoic stromatoporoid species was presented by YAVORSKY (1951). This was useful for generalized correlation across the former Soviet Union (mainly Russia), with many of the species

listed by YAVORSKY exhibiting series-length (or epoch-duration) time ranges (that is, restricted either to the middle Silurian, Middle Devonian, or Upper Devonian). YAVORSKY (1929, 1955, 1957, 1961, 1962, 1963, 1965, 1967), RIABININ (1936, 1937, 1939, 1941, 1951, 1953), and GORSKY (1938) also demonstrated the value of stromatoporoids as generalized guide fossils for regional geological exploration work in the Ordovician, Silurian, and Devonian successions of the former Soviet Union.

LECOMPTE (1951 in 1951–1952), in a monographic treatment of the Devonian stromatoporoid species from the Ardennes of Belgium, also included a tabular presentation of species data—recognizing about half of the 115 species as being confined to 1 of the 5 main stratigraphic subdivisions (Couvinian 1 substage, Couvinian 2 substage, Givetian stage, Frasnian 1 substage or Frasnian 2 substage)—but he did not provide any further biostratigraphic details. Similar tables of the species distribution were presented by RIABININ (1951, 1953) for the local stages (horizons) of the Silurian in Estonia and Podolia (Ukraine).

The view that the stromatoporoids were biostratigraphically important fossils was first clearly proposed by GALLOWAY and ST. JEAN (1957, p. 31, 85) in their monographic treatment of Middle Devonian stromatoporoids from the central United States. They suggested that stromatoporoids were likely to prove to be zonal fossils, as useful in the Devonian as the trilobites were in the Cambrian, or the graptolites in the Ordovician! FLÜGEL (1959, table 25) emphasized the stratigraphic importance of stromatoporoid genera. His range chart, based mainly on GALLOWAY's (1957) taxonomy, showed that many of the genera were restricted to either the Ordovician or the Devonian. FLÜGEL stressed that a number of genera and species could be viewed as index fossils for the Devonian, especially the Middle Devonian. FLÜGEL (1962) also presented a general review of the biostratigraphic significance of stromatoporoid faunas in the Silurian and Devonian.

In the 1960s and 1970s, Silurian stromatoporoid faunas of different regions were described, and the stratigraphic distribution of species was recorded. This description and stratigraphic placement opened the possibility of using stromatoporoids in local stratigraphy and increased their value for correlating stratigraphic sequences. NESTOR (1964a, table 2, 5; 1966a, table 2, 4) published range charts of genera and species distributed in regional stages of the Upper Ordovician and Silurian of Estonia and commented on the occurrences of some species from other areas. MORI (1968, table 1; 1970, table 1) published range charts of stromatoporoid species in the stratigraphic units of the Wenlock and Ludlow strata on Gotland (Sweden), and roughly correlated the stratigraphic successions of Gotland and Estonia using the assemblages of species in common. MORI (1978, table 1) also presented the stratigraphic distribution of Silurian stromatoporoids from the Oslo area, Norway, and compared them with the Gotland and Estonian stromatoporoid successions. BOL'SHAKOVA (1973, p. 19–20) recorded the stratigraphic distribution of stromatoporoid species in the Silurian sequence of Podolia. BOGOYAVLENSKAYA (1973a) described the Silurian stromatoporoids from different districts of the Urals and used common species for correlation of stratigraphic units.

In North America, Ordovician–Silurian stromatoporoids of Anicosti Island, eastern Canada, were described by NESTOR, COPPER, and STOCK (2010, fig. 4–5), and other Silurian stromatoporoids were documented from eastern Quebec and from Somerset Island of Arctic Canada (SAVELLE, 1979). All of these works included range charts. Also, NESTOR (1976) authored a monograph on Ordovician and Silurian stromatoporoids from the Siberian platform and additionally distinguished a succession of species assemblages.

The stratigraphic ranges of species have also been used to establish correlations of the Devonian rocks. MISTIAEN (in BRICE & others, 1977) presented a table of ranges

for the Ferques section in the Boulonnais area of northern France and compared the occurrences with those in the Ardennes of Belgium and in other countries. In addition, MISTIAEN (1980) described the species from the Ferques section, recognized 13 levels characterized by distinctive stromatoporoid faunas, and compared the faunas with those in the stratigraphic sections through the Givetian interval of the Ardennes described by LECOMPTE (1951 in 1951–1952). MISTIAEN (1982) also analyzed the distribution of faunas around the Givetian–Frasnian boundary in the Boulonnais, Ardennes, Poland, and the Czech Republic. In 1988, he recognized there were 3 stromatoporoid-based Givetian zones and 2 in the Frasnian part of the Boulonnais section.

MISTIAEN (1985) also showed the distribution of Devonian stromatoporoid species in the reefal complexes of the Central Mountains of Afghanistan. He presented tables showing distributions of stromatoporoid species in a number of stratigraphic sections, as well as the overall Devonian ranges of taxa, with ties to the main global conodont, graptolite, and other biozonations. The Middle Devonian fauna in particular is closely related to counterparts in the Ardennes (LECOMPTE, 1951 in 1951–1952) and the Boulonnais area (MISTIAEN in BRICE & others, 1977; MISTIAEN, 1980, 1982, 1988). The correspondence of European stratigraphic ranges with those of Afghan taxa confirmed that the stromatoporoids were both members of the same comparatively wide-ranging, provincial Old World Realm. Less close relationships exist with other so-called Old World faunas in other regions, such as the Czech Republic (ZUKALOVA, 1971; MAY, 2005), the Kuznetsk Basin (Siberia), southern China, and Australia. MISTIAEN (1985, fig. 17–18) was able to determine the age relationships of the discrete reefal complexes to within a Devonian stage, based on the overlapping stratigraphic ranges of the stromatoporoid faunas (36 species belonging to 19 genera), at least through the Emsian to early Frasnian interval.

The documentation of stromatoporoïd faunas in China commenced mainly following the discoveries of abundant faunas during the nationwide geological surveys and stratigraphic work from 1949 onward (YANG & DONG, 1962). Through the 1970s and 1980s, numerous species were described from the Middle Ordovician to Upper Ordovician, lower Silurian, and especially from the rich assemblages through the Devonian of southern China (DONG & YANG, 1978; YANG & DONG, 1979; DONG, 1982; DONG & WANG, 1982; DONG & WANG, 1984; WANG, DONG, & FU, 1986; WANG, 1988; DONG, 2001). Some of these assemblages were useful for correlation and/or for establishing age relationships of particular stromatoporoid-bearing successions. Several of the above-cited publications included tabular presentations of species ranges: for example, through the Middle Ordovician to Devonian successions of the Xinjiang Autonomous Region (northwestern China) by DONG and WANG (1984), and the Devonian sequences in southern China: parts of Guangxi province by YANG and DONG (1979) and Sichuan province by WANG (1988).

NESTOR and STOCK (2001) presented range charts of the distribution of genera in North America and Baltoscandia as part of a discussion of the extinction of stromatoporoid faunas leading up to the end-Ordovician glaciation, and then their recovery through the early Silurian (Llandovery), including their generalized spread into other regions, such as Ireland, Novaya Zemlya, the Siberian Platform, and the Yangtze Platform.

Where stromatoporoid generic ranges were well understood, for example, in the Devonian (as shown by STEARN, 1979, fig. 1), the data could be plotted in a range chart for broad-scale correlation work. In this chart, most of the Devonian is divided into stage-age subdivisions (the exception being the Lower Devonian series-epoch couplet). Many Devonian genera are long ranging, through more than one stage-age interval, but a few short-ranging (key) genera are also represented, such as *Araneosustroma*,

encompassing the Lower Devonian series; *Pseudoactinostroma* in the Eifelian stage; *Columnostroma* in the Givetian; and *Bullulodictyon*, *Arctostroma*, *Styloporella*, and *Euryamphipora*, in the Frasnian. Other slightly longer-ranging genera also have correlation potential because their first and/or last appearances coincide with particular stage (or series) boundaries. Remarks on the patterns of development of the Lower Devonian faunal successions were also presented by WEBBY, STEARN, and ZHEN (1993, fig. 4). In the figure, first and last appearances of key, short-lived genera characterize boundaries between the Lochkovian, Pragian, and lower Emsian. The scheme provides a broad basis for identifying diagnostic stromatoporoid assemblages to stage level.

We here present a set of range charts to show the stratigraphic distribution of genera worldwide (Fig. 362–364). Although the genus is, in taxonomic usage, a more artificial concept than species, it provides a reasonable means of attaining broadly based global correlations employing stratigraphic ranges.

The first stromatoporoids were the labechiids (Fig. 362; see p. 709–753); they remained the dominant group through the Mid–Late Ordovician, but declined through the Silurian, with few persisting into the Early–Mid-Devonian, and then showed a resurgence during the Late Devonian. In general, the genera do not seem to have much biostratigraphic potential (Fig. 362), though within the Ordovician the assemblages exhibit some successional changes, from associations of morphologically simpler families Rosenellidae, Labechiidae, and Aulaceratidae taxa in the Darriwilian, to the more complex, skeletal meshworks of some genera of the families Stromatoceriidae, Platiferostromatidae, and Stylostromatidae, with mamelon columns and flanged pillars in the Late Ordovician and early to mid-Silurian. A number of labechiids in the Late Devonian (Famennian), such as the platiferostromatids (*Platiferostroma*, *Vietnamostroma*) and more specialized stylostromatids (*Pennastroma*,

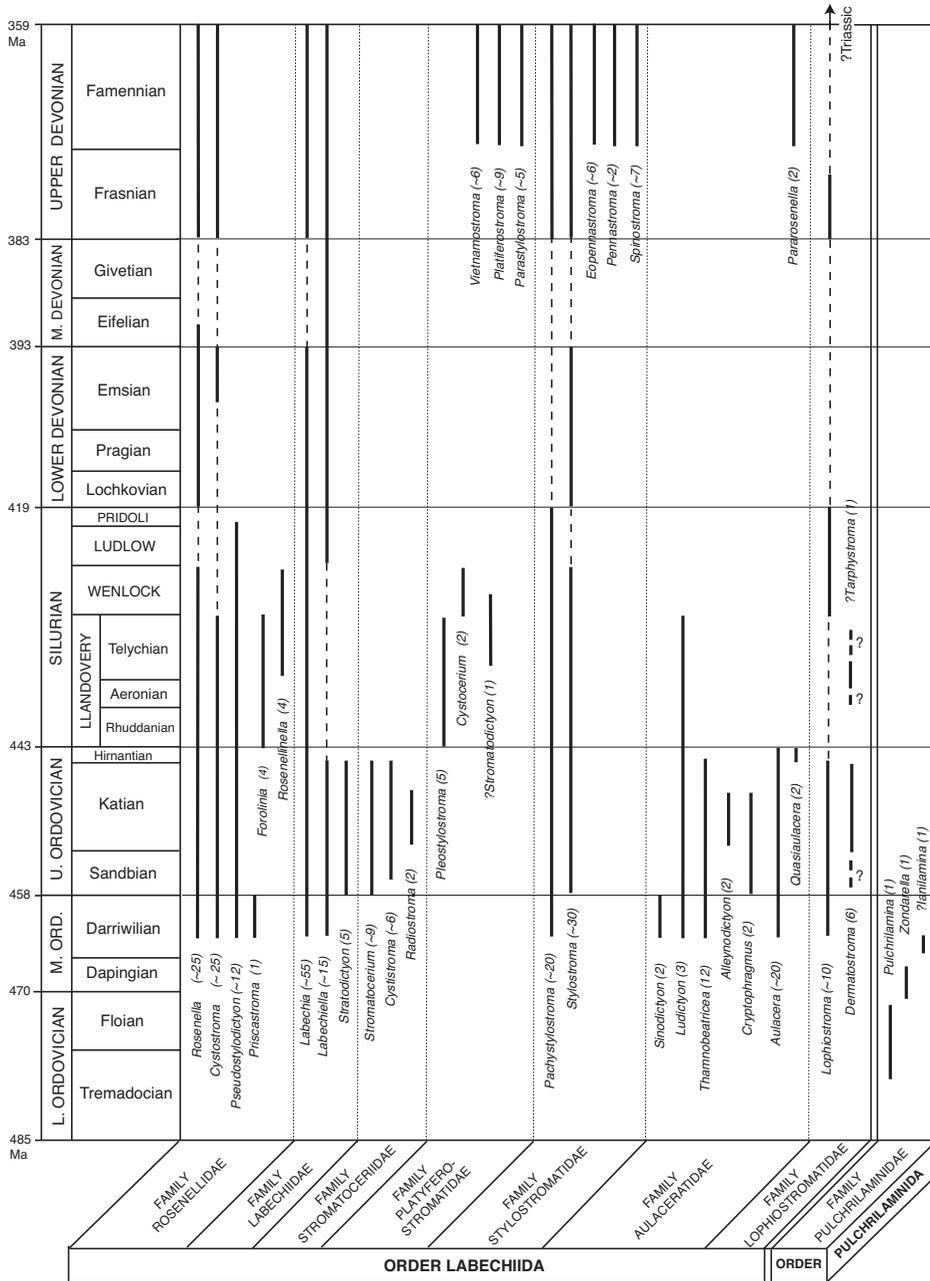


FIG. 362. Stratigraphic ranges of the labechiid genera of the class Stromatoporoidea and the pulchrilaminid genera of the class Uncertain (see Class Uncertain, Order Pulchrilaminida, p. 837–844); *fine dashed lines* depict apparent gaps in the continuity of the record; *thick dashed line* with a question mark signifies a doubtful extension of a taxon range (e.g., range of *Dermatostroma*); note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history; *Lophiostroma* is the only labechiid genus to have a possible post-Paleozoic record, here shown with an *upwardly directed arrow* and of ?Triassic age (see Boiko, 1970a). Note also that Stearn and Stock (p. 310) listed *Lophiostroma* as an excluded taxon for calcareous crusts in the upper Paleozoic of Japan (adapted from Webby, Stearn, & Nestor, 2012; time scale after Gradstein & others, 2012).

*Spinostroma*), show further differences that may have some correlation potential.

Two of the present authors (STEARN and WEBBY) have very different explanations for the late Silurian to Mid-Devonian decline then Late Devonian resurgence of the labechiids. STEARN considers that some of the genera, for example, *Labechia*, *Stylostroma*, and *Pachystylostroma*, have such long and discontinuous ranges as to suggest that their Late Devonian representatives are not directly descended from their Ordovician precursors, but evolved anew from some persistent rootstock; in other words, they represent Elvis taxa (ERWIN & DROSER, 1993). The almost complete absence of labechiids from the Eifelian–Givetian interval, when other stromatoporoids reached their greatest diversity, supports this hypothesis. STEARN also suggests that the uncommon Mid-Devonian occurrences of labechiids may be misidentifications of simple cystose structures common in the space-filling strategies of other fossil organisms (rugosans, tabulates, hydrozoans, bryozoans, mollusks) (ST. JEAN, 1986, p. 1053, commenting on STEARN, 1983a).

On the other hand, WEBBY prefers to regard the patterns of disappearances and reappearances of labechiid genera through the Silurian to Late Devonian as representing Lazarus taxa—that the gaps in the continuity of the labechiid records are artifacts of their relatively poor preservation and low diversity. A number of labechiids were found in well-exposed and dated reefal sequences of Lockhovian–Pragian and Emsian–Eifelian ages of the Broken River region of Queensland by WEBBY and ZHEN (1997); that is, from intervals that were previously represented by gaps in the continuity of the labechiid record. These Lockhovian–Pragian (species of *Cystostroma* and *Labechiella*) and late Emsian–early Eifelian labechiids (species of *Stylostroma* and *Rosenella*) form a sparse, poorly preserved component of associations that are dominated by richly diverse and well-preserved nonlabechiid stromatopo-

roids. In other words, the poorly preserved minor component of labechiids was only found at the various localities because of the high quality of the exposures available for study. It is considered likely that the labechiid component may be difficult to find in less well-preserved successions, leaving only the dominantly, less altered nonlabechiids for study. The Broken River example is instructive in demonstrating that labechiids were continuing to live in associations with Early to earliest Mid-Devonian nonlabechiids, and they may yet prove to form part of a more or less continuous line of labechiid descent from Ordovician precursors into the Late Devonian. More intensive collecting and study of sequences (especially Devonian carbonate) is expected to bridge the gaps in continuity of the labechiid record prior to the Late Devonian.

The clathrodictyids have their roots in the Late Ordovician (*Clathrodictyon*, *Ecclimadictyon*) (Fig. 363; and see Clathrodictyida, p. 755–768). They reached their peak of diversity in Silurian time were numerous also in the Early and Middle Devonian, but only a few persisted to the end of the Devonian. Many genera are relatively long ranging and almost cosmopolitan (*Clathrodictyon*, *Ecclimadictyon*, *Gerronostromaria*, *Petridiostroma*), but some rare and peculiar forms (*Bullulodictyon*, *Gerronodictyon*, *Belemnostroma*) also occur. The representatives of the families Clathrodictyidae and Gerronostromatidae are widespread in both Silurian and Devonian rocks, but most of the representatives of the family Actinodictyidae are restricted to the Silurian. On the other hand, the representatives of the families Atelodictyidae and Tienodictyidae mostly occur in Devonian rocks. They include such genera as *Anostylostroma*, *Atelodictyon*, *Pseudoactinodictyon*, and others that are valuable for correlation.

The generic diversity of the actinostromatids peaked in the middle of the Silurian, when a rapid evolutionary radiation took place in the families Pseudolabechiidae, Actinostromellidae, and Densastromatidae

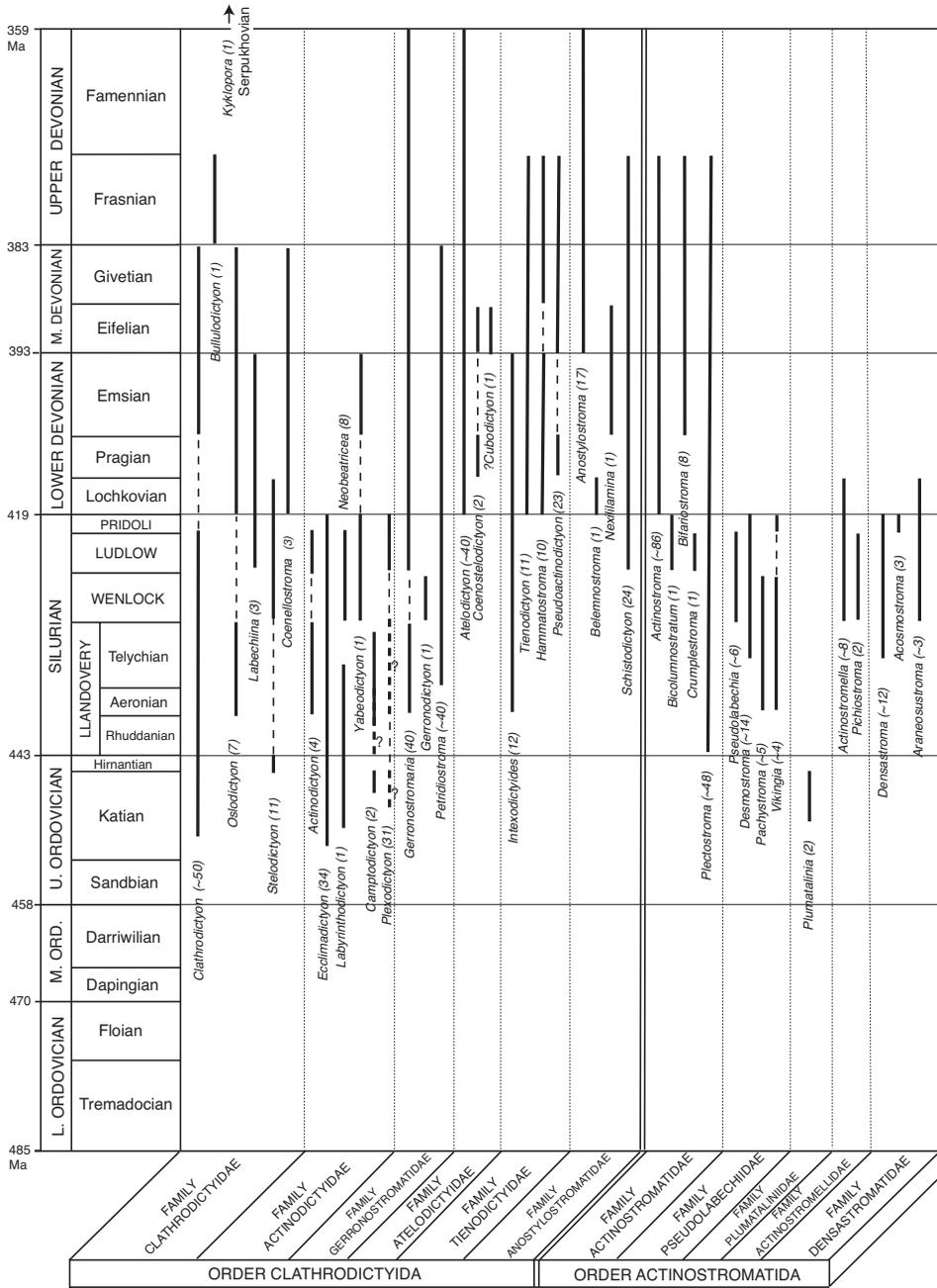


FIG. 363. Stratigraphic ranges of clathrodictyid and actinostromatid stromatoporoid genera of the class Stromatoporoidea; *thick dashed lines with question marks* signify doubtful extensions of taxon ranges; *fine dashed lines* depict apparent gaps in the continuity of record; note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history; *Kyklopora* is the only genus that has a restricted post-Devonian record, with a limited occurrence in the lower Carboniferous (Serpukhovian stage), according to NESTOR (see p. 755) (adapted from Webby, Stearn, & Nestor, 2012; time scale after Gradstein & others, 2012).

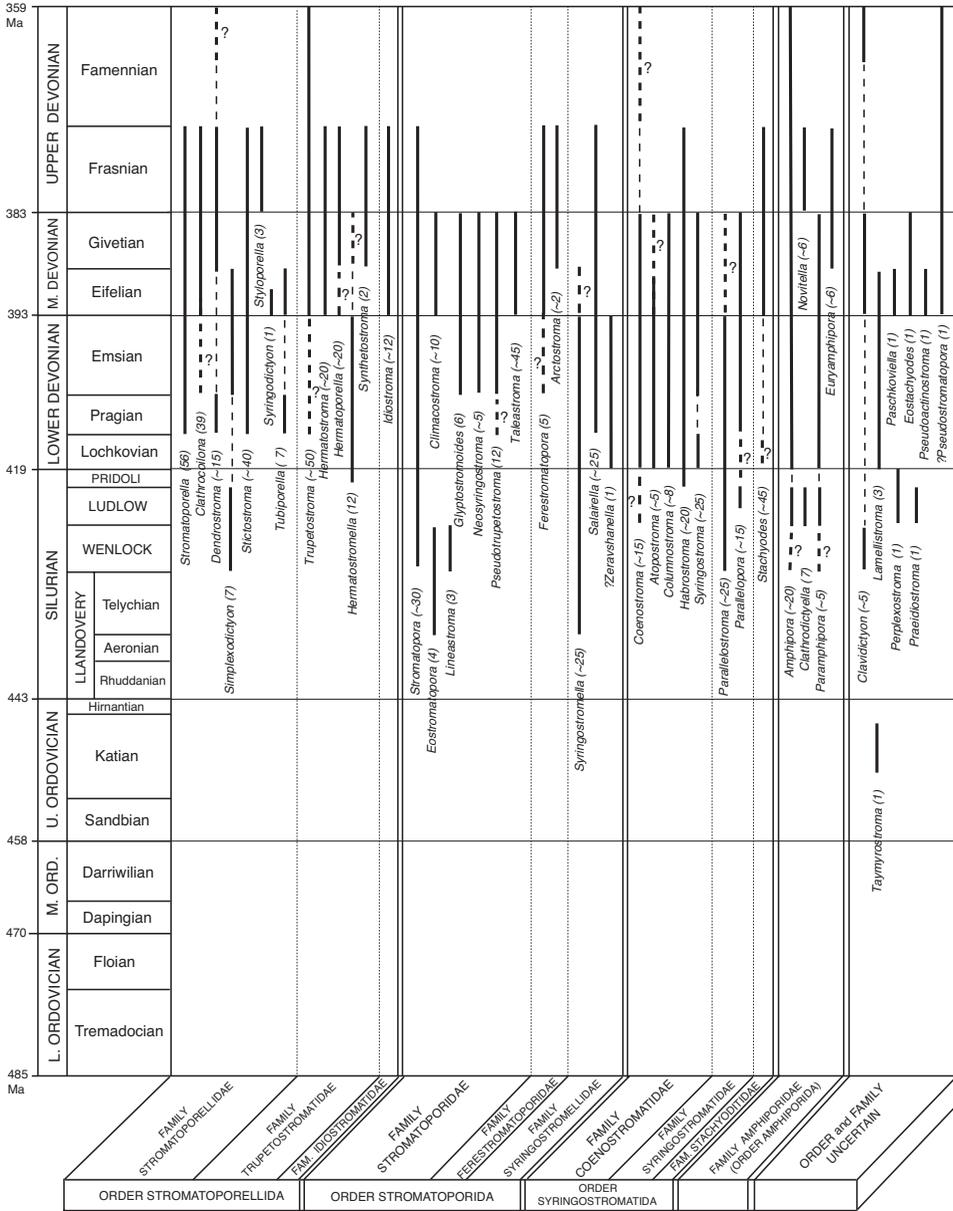


FIG. 364. Stratigraphic ranges of stromatoporellid, stromatoporid, and syringostomatid stromatoporoid genera, as well as representatives of order and family Uncertain of the class Stromatoporoida; *thick dashed lines with question marks* signify doubtful extensions of taxon ranges; *fine dashed lines* depict apparent gaps in the continuity of record; note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history (adapted from Webby, Stearn, & Nestor, 2012; time scale after Gradstein & others, 2012).

(Fig. 363; see p. 769–779). Only a few genera (*Actinostromella*, *Araneosustroma*) of these families range into the Lochkovian. Comparatively short-ranging genera include stratigraphically valuable species, for example, index species of such Baltoscandian stromatoporoid communities as *Vikingia tenuis*, *Araneosustroma stelliparratum*, and *Actinostromella vai-verensis* (NESTOR, 1999b). Three of the most common genera of actinostromatids (*Actinostroma*, *Bifariostroma*, *Plectostroma*) belong to the family Actinostromatidae and are the main representatives of actinostromatids in the Devonian.

The orders Stromatoporellida, Stromatoporida, and Syringostromatida mainly include Devonian taxa with a few genera (*Simplexodictyon*, *Stromatopora*, *Syringostromella*, *Parallelostroma*) originating in the Silurian (Fig. 364; see p. 781–824). Among the stromatoporellids, such genera as *Clathrocoilona*, *Stictostroma*, *Stromatoporella*, *Trupetostroma*, and *Hermatostroma* are the most characteristic of this almost cosmopolitan fauna. Most of the common stromatoporellid genera extend through the Eifelian–Frasnian acme of stromatoporoid diversity. Rather similar are the ranges of the stromatoporids. Such genera as *Climacostroma*, *Glyptostromoides*, *Neosyringostroma*, *Taleastroma*, and *Pseudotrurpetostroma* appear to have biostratigraphic potential, but the genus *Stromatopora* itself has a very long range from the Ludlow to Famennian. Some earlier records of *Stromatopora* are now treated as representatives of *Lineastroma* and *Eostromatopora* (NESTOR, 1999a). The family Syringostromatidae was characteristic of the Early Devonian and Eifelian. The acme of the family Coenostromatidae was also in the Early Devonian, but *Parallelostroma* appeared earlier in the Wenlock and *Habrostroma* in the Pridoli. *Atopostroma* may prove to be an excellent indicator of Lower Devonian rocks, though the presence of the genus in a reefal deposit of Givetian age in Afghanistan (MISTIAEN,

1985) remains an anomaly. Difficulties in recognizing the genera of the Amphiporidae limit their usefulness for biostratigraphy (Fig. 364; see p. 824–829).

It should also be noted that there are two “stromatoporoid” genera with post-Devonian records, one supposedly a labechiid referred to the genus *Lophiostroma*, implying it formed part of an extended range until the Triassic (see Fig. 362; see p. 751–752), and the other is the clathrodictyid genus *Kyklopora* (see p. 755–757) recorded only from the Carboniferous (Upper Mississippian, Serpukhovian Stage, see Fig. 363); no earlier record of this form is known. It remains uncertain whether these post-Devonian records represent convergences derived from different “stromatoporoid-type” stocks (e.g., Introduction to Post-Devonian Hypercalcified Sponges, p. 193–208) during the upper Paleozoic to Mesozoic (i.e., an Elvis taxon of ERWIN & DROSER, 1993), or, whether, at least in the case of *Lophiostroma*, it reappeared in the Triassic as a Lazarus taxon at the end of its range in a long-lived, more or less continuous line of descent from Middle Ordovician precursors.

### BIOSTRATIGRAPHIC STANDARDS BASED ON CONCURRENT COMMUNITY SUCCESIONS

NESTOR (1982, 1984, 1990b) adopted a novel approach to establishing a biostratigraphic standard for Late Ordovician to Silurian stromatoporoid faunas in the Baltic-Scandinavian region, based on the spread of assemblages across a full range of onshore to offshore environments, from lagoonal, to shoal and reef, to open shelf, and into some slope habitats (Fig. 365). Later, NESTOR (1999b) linked the associations (communities) of stromatoporoids with the standard benthic assemblages (BA1–BA5) of BOUCOT (1975). The complete spectrum of laterally equivalent associations was particularly well developed in the Silurian rocks.

Associations of taxa in the open shelf, reef, and shoal facies, representing BOUCOT's BA2–4 assemblages, were more diverse, temporally shorter-ranging, and spatially more widely distributed. The more cosmopolitan, open shelf taxa were considered by NESTOR (1999b) to have the greater potential for use in the stromatoporoid biostratigraphy, because they had geographically wider ranges. Examples in the Llandovery include the *Clathrodictyon boreale*–*Ecclimadictyon microvesiculosum* community, which is moderately diverse, spans two regional stages, and spreads laterally into both open shelf and shoal lithofacies. Its two name-bearing species have been recorded from the same interval in many parts of the world, including Anticosti Island (Canada; NESTOR, COPPER, & STOCK, 2010, p. 22). The succeeding *Clathrodictyon variolare* community is also diverse, characteristic of the open shelf, and has a short time range (only part of one regional stage); and typical elements of the community (*C. variolare*, *Ecclimadictyon fastigiatum* [= *Camptodictyon penefastigiatum* NESTOR, COPPER, & STOCK, 2010], *Stelodictyon conodigitatum*) are widely recognized elsewhere (e.g., Norway, Novaya Zemlya, Anticosti Island, Iowa, Alabama). The stromatoporoid assemblages at opposite ends of the environment spectrum—in the lagoon (BA 1) and the deeper marginal shelf to slope (BA 4/5)—were the least diverse and had the longest ranges in time.

A community-based approach was also applied by NESTOR (1999b) to establish the Late Ordovician stromatoporoid faunal succession in Baltoscandia, but no lateral equivalents were recognized, as in the Silurian succession. The six temporally distinct Late Ordovician examples comprise: (1) the reef (shoal)-type assemblages with labechiids in the Oandu stage of Estonia and Mjøsa Formation of Norway (early Katian); (2) the first clathrodictyids with some labechiids in the above-storm-base, open-shelf assemblages of the Vormsi to early Pirgu (i.e., from mid- to late Katian) in Estonia; and (3) some clathrodictyids and labechiids again in

the reef (shoal)-type assemblages of the late Pirgu to Porkuni (late Katian to Hirnantian) interval of Estonia and Norway.

The development of NESTOR's (1999b) laterally equivalent, community-based correlation scheme was based primarily on the more complete Silurian successional record of stromatoporoid faunas across the Baltic-Scandinavian region. This record was derived largely from the major documentation of the Silurian stromatoporoid faunas by NESTOR (1964a, 1964b, 1966a) in Estonia, and by MORI (1968, 1970, 1978) from the Island of Gotland (Sweden) and the Oslo region of Norway. In Estonia, NESTOR (1964a, 1964b, 1966a) recognized 65 valid Silurian stromatoporoid species belonging to 20 genera, he revised RIABININ's (1951) earlier work on the faunas and outlined a broadly based, fivefold, stromatoporoid species-based, assemblage zonation that more or less paralleled the existing tabulate coral zonation. The Llandovery (Juuru, Raikküla, and Adavere regional stages) was divided into three stromatoporoid zones. Broadly based zonal indices for the Wenlock (Jaani to Jaagarahu stages) and Ludlow (Paadla and Kuressare stages) intervals were characterized by a species name bearer and other diagnostic index fossils. The units including reefs, such as those included in the Llandovery (upper Juuru), Wenlock (Jaagarahu), and Ludlow (Paadla) stages, were particularly rich in species. However, the lack of detailed studies of Silurian stromatoporoids in other areas prior to the late 1960s prevented these broadly based stromatoporoid zonal indices being used for wider-ranging correlation, except for one example establishing a tie, based on stromatoporoids between the lower Ludlow Paadla stage of Estonia and the Malinovetsky Horizon of Podolia, southwestern Ukraine (NESTOR, 1966a, p. 73).

The Silurian stromatoporoids that occur abundantly through the Gotland reefal and nonreefal successions in Sweden were studied by MORI (1968, 1970). Sixty-eight species belonging to 24 genera were described. The ranges of the species were relatively short,

GLOBAL SUBDIVISIONS	BALTIC SCANDINAVIAN STAGES		FACIES BELTS					
			LAGOON	SHOAL	OPEN SHELF		"SLOPE"	
			STANDARD BENTHIC ASSEMBLAGES					
			BA1/2	BA2	BA3	BA4	BA4/5	
PRIDOLI	OHESAARE							
	KAUGATUMA		<i>Parallelostroma tuberculatum</i>		<i>Actinostromella vaiverensis</i>			
LUDLOW	IGORS- LUDFOR- TIAN	KURESSAARE	<i>Plexodictyon irregulare</i>					
		PAADLA	<i>Araneosustroma stelliparratum</i>	<i>Simplexodictyon podolicum</i> <i>Stromatopora bekkeri</i>		<i>Parallelostroma typicum</i> – <i>Lophiostroma schmidtii</i>		<i>Densastroma densum</i>
		ROOTSIKÜLA		<i>Parallelostroma tenellum</i>				
WENLOCK	HOME- RIAN	JAAGARAHU	<i>Labechia conferta</i> <i>Stromatopora pseudotuberculata</i>		?			
		JAANI	<i>Ecclimadictyon astrolaxum</i>					
			<i>Vikingia tenuis</i>		<i>Densastroma pexisum</i> – <i>Petridiostroma simplex</i>			
LLANDOVERY	AERO- NIAN	ADAVERE	<i>Plectostroma norvegicum</i>		<i>Eostromatopora impexa</i>			
		RAIKKÜLA	<i>Eostromatopora ringerikensis</i>					?
			<i>Clathrodictyon variolare</i>					
		JUURU	<i>Intexodictyides avitum</i> <i>Pachystylostroma ungerni</i>		<i>Clathrodictyon boreale</i> – <i>Ecclimadictyon microvesciculosum</i>		<i>Forolima brevis</i>	
UPPER ORDOVICIAN	KATTIAN-HIRNANTIAN	PORKUNI	<i>Clathrodictyon gregale</i>					?
		PIRGU	<i>Stylostroma-Pachystylostroma</i>					
		VORMSI	<i>Clathrodictyon microundulatum</i> <i>Clathrodictyon vormsiense</i>					
		NABALA						
		RAKVERE	<i>Pachystylostroma mammillatum</i>					
		OANDU	<i>Stromatocerium sakuense</i>					

FIG. 365. Diagrammatic representation of biostratigraphically useful, laterally equivalent, stromatoporoid assemblages of Upper Ordovician–Silurian sequences of Baltoscandia across the main facies belts of Nestor's (1990b) Paleobaltic basin, and Boucot's (1975) Standard Benthic Assemblages (BA) (adapted from Nestor, 1999b).

confined to one or two stratigraphic units within the Wenlock or Ludlow (see MORI, 1968, table 1; 1970, table 1), possibly due to facies constraints. Nevertheless, approximately one-third of these species are known to occur also in Estonia and provide a useful means of biostratigraphic correlation, at a number of different levels, through respec-

tive Wenlock and Ludlow successions (see MORI, 1968, table 2; 1970, table 4).

In addition, MORI (1978) undertook a comparative survey of Silurian stromatoporoid assemblages from the Oslo region (Norway) in order to reveal their relationships to contemporaneous occurrences in Estonia and Gotland. Of the 15 species,

10 are from the Llandovery, 3 are from the Wenlock, and the remaining 2 are probably from the Ludlow. Two-thirds of the species are found in other areas of the Baltic (Estonia, Gotland). However, MORI's (1978, table 1) stratigraphic distribution chart shows that not all these common occurrences are strictly coeval.

Through the past three decades, NESTOR (1982, 1984, 1990a, 1999b) has refined the biostratigraphy of the Baltic Silurian on the basis of community associations. He noted that parallel shallower and deeper-water communities could be differentiated within the respective stromatoporoid zonal successions and suggested that the succession of shallower associations may prove suitable as a zonal standard for use in Balto-Scandinavia and further afield. In 1982, NESTOR defined five superposed, shorter-ranging, shallow-water associations (*Eostromatopora impexa*, *Vikingia tenuis*, *Ecclimadictyon astrolaxum*, *Labechia conferta*, and *Parallelostroma tenullum* communities), and two laterally equivalent, longer-ranging, deeper-water associations (*Densastroma pexisum* and *D. densum* communities) in the Wenlock and Ludlow (Fig. 365). Additionally, he identified a restricted nearshore association dominated by *Araneosustroma stelliparatum* in the late Wenlock of Estonia that represents a lateral equivalent of the normal shallow-water association of the *P. tenullum* community on Gotland. A detailed log of the stromatoporoid species, through the 29-m-thick, lower Wenlock biostratigraphic reference section of Vattenfallet, close to Visby (Gotland), identifying representatives of the *Eostromatopora impexa* community in the upper Visby Marl, and members of the *Vikingia tenuis* community in overlying beds of the Högklint Limestone (Fig. 365), was also contributed (NESTOR, 1979).

A more complete listing of the distribution of stromatoporoid taxa in the Silurian of Estonia was presented in NESTOR (1990a), together with a more comprehensive subdivision of the community-based zonation of stromatoporoids across lower energy

lagoonal, high-energy shoal (or reefal), lower energy, open shelf, and slope facies belts (NESTOR, 1984, 1990a). In the latter work, the complete list of the Upper Ordovician and Silurian stromatoporoid species from Estonia and Sweden was published, including 104 species belonging to 25 genera. The genera, except for *Clathrodictyon* and *Ecclimadictyon*, exhibit only moderate levels of species diversification. Species of *Clathrodictyon* and *Ecclimadictyon*, especially those from the Llandovery interval, have records of 13 and 10 species, respectively; that is, they were relatively much more diverse than the rest. This suggests that the taxa have been oversplit, and that it would be useful, at least for biostratigraphic purposes, to have them reevaluated using a broader species concept, as in the study undertaken recently by NESTOR, COPPER, and STOCK (2010).

An updated version of the community-based biostratigraphic standard of the Baltic-Scandinavian Silurian stromatoporoids was presented by NESTOR (1999b), with the addition of supplementary data from Norway. As a result, 22 different successive and concurrent Silurian stromatoporoid communities were defined (see Fig. 365). The succession is most completely developed in the onshore, high-energy shoal (or reef) facies that occupies the position of BOUCOT's (1975) Benthic Assemblage BA2, with the species represented by the most diverse, short-ranging forms. NESTOR (1999b) further noted that some 99 species have now been recorded through the Baltic-Scandinavian Late Ordovician to Silurian succession in the shoal reef (BA2 position), as compared with 49 species in the inner open shelf (BA3 position). The combined, relatively diverse, short-ranging shoal and inner open shelf assemblages provide the best composite basis for establishing the biostratigraphic standard, with potential use for correlating sequences well beyond the Baltic-Scandinavian region.

NESTOR's (1999b) Silurian reef and shoal assemblages were the most diverse,

and though the taxa exhibited the shortest time ranges, they unfortunately had mainly narrower spatial distributions. Therefore, these shorter-range, more specialized, reef and shoal species were not as useful for establishing interregional correlations, but they were still important for determining the spatial and temporal relationships of reefs and shoals in the Baltic-Scandinavian region and, less commonly, based on a few species, farther afield. NESTOR (1990b) also demonstrated in a global biogeographic survey of Silurian stromatoporoid genera that very limited evidence of provincialism exists. Consequently, the impact of provincialism on species-based correlations is probably minimal.

NESTOR's (1999b) approach to establishing a laterally equivalent, community-based, biostratigraphic standard, using the Silurian stromatoporoid succession in the Baltic-Scandinavian, is a good model for application to other continental platform regions of the world, for example, in North America and China. In these regions, as in Balto-Scandinavia, there is a wide range of well-exposed Paleozoic stromatoporoid-bearing carbonate successions available for study across a range of onshore to offshore environments and the potential to closely tie such regional, community-based stromatoporoid zonal indices to well-established and highly resolved zonal schemes based on other fossil groups such as conodonts and graptolites (see below).

## LINKAGES WITH OTHER ZONATIONS

The comparison of zonal successions based on different fossil organisms is an essential part of the work of the biostratigrapher. An unrivaled succession of 28 named conodont zones has been established for worldwide correlation of Devonian rocks (ZIEGLER & KLAPPER, 1985), but zonal schemes based on stromatoporoid taxa remain at a much more rudimentary stage of development. STEARN's (1997a, 2001) biostratigraphic work on the stromatoporoid assemblages of the Devonian

reef-bearing carbonate succession in Western and Arctic Canada has already demonstrated the group's value for correlation across North America and their potential for wider-ranging, perhaps global, correlation of the reef facies. Because diagnostic conodonts rarely occur in reefs, precise stratigraphic relationships must be established between the stromatoporoid assemblages and the diagnostic conodont zones of the laterally equivalent strata. Conodont work in Western and Arctic Canada by UYENO (1974, 1990, 1991), UYENO and KLAPPER (1980), and others permits the age relationships of the stromatoporoid-bearing reefs to be assigned to a particular part of the conodont zonal succession (Fig. 366).

STEARNS (1997a, 2001) regarded all ten stromatoporoid assemblages spanning the Devonian as having value for correlation in North America, and more than half the assemblages (those extending through the Lower Devonian, lowermost and uppermost Givetian, and Famennian intervals) as having wider, intercontinental, correlation potential. STEARN (2001) included a range chart showing the ranges of diagnostic species for each assemblage. This work involved adopting a broader species concept than previously and placing a large number of previously described species (about 50%) in synonymy. His approach recognized that the complex skeletons of stromatoporoids exhibit a far wider variability than was thought previously. The assemblages define some time units that range through entire stage divisions and others that are of substage duration. Most of the listed species (STEARNS, 2001, fig. 1) have comparatively short time ranges.

PROSH and STEARN (1996) presented in greater detail the Emsian-early Eifelian records of stromatoporoid ranges (a fauna comprising 25 species in 22 genera) from Arctic Canada, with ties to the well-established, standardized, conodont zonation. Nearly half the Arctic species are common to other regions (eastern North America, Asiatic Russia, southeastern

Australia, and China). More than half the species span more than one conodont zone (within the Emsian–earliest Eifelian interval), but one third of the species exhibit very short stratigraphic ranges, of approximately one conodont zone.

Additionally, PROSH and STEARN (1993, 1996) asserted that a number of the species from Arctic Canada allowed precise correlation with faunas described by GALLOWAY and ST. JEAN (1957) and FAGERSTROM (1982) from the midcontinental United States. In particular, occurrences of four stromatoporoid species [*Stromatoporella perannulata* GALLOWAY and ST. JEAN; *Stictostroma gorriense* STEARN; *Habrostroma proximlaminatum* (FAGERSTROM); and *Parallelopora campbelli* GALLOWAY & ST. JEAN] in the Blue Fiord succession of the Arctic, which is well dated by conodonts, and in the Detroit River Group of the Michigan Basin, have led to the proposal that the Detroit River Group is entirely Emsian, rather than Eifelian, in age, and the conodont dating for this group has been misinterpreted (PROSH & STEARN, 1993, 1996). However, KLAPPER and OLIVER (1995) disputed this correlation on the basis that the conodonts of the Detroit River Group and correlatives in eastern North America are of Middle Devonian age, and two of the four stromatoporoid species have ranges extending up into the Eifelian. They claimed the stromatoporoid species had diachronous relationships—that they needed a long time to migrate from the Arctic to the eastern regions of America because of biogeographic barriers (but see PROSH, 1995, for counterarguments).

In summary, STEARN (1997a, 2001) has suggested that the Devonian succession of Arctic and Western Canada could be divided into ten biozones on the basis of distinctive stromatoporoid faunas (Fig. 366). He proposed that the stromatoporoids of these ten assemblages could form the basis of correlation between reef successions on the continental and perhaps intercontinental scale. The restriction of certain species to narrow time intervals and their wide geographic

extent gave hope, in his view, that stromatoporoid biostratigraphy would be as effective in the reef facies as the graptolites have proven to be in the black shale facies. At present, this goal has not been attained and will not be until the data on stratigraphic distribution are brought together with a consistent taxonomy and within the context of a much more complete knowledge of global patterns of provincial change through Devonian time.

## OTHER BIOSTRATIGRAPHIC RECORDS

### ORDOVICIAN AND SILURIAN

WEBBY (1969) introduced three informal subdivisions based on diagnostic coral and stromatoporoid assemblages for correlation of the Upper Ordovician island-arc carbonate successions of the Molong Volcanic Belt, central New South Wales (NSW), Australia. Fauna I included a number of distinctive labechiids, and Faunas II and III were characterized by the first appearances of clathrodictyids and continued presence of other labechiids. PICKETT (1985a) recognized an older, pre-Fauna I assemblage (with earlier labechiids) in the adjacent Junee-Narromine Volcanic Belt, and PICKETT and PERCIVAL (2001) later replaced WEBBY's numbered stromatoporoid assemblages with four, formalized, composite coral/sponge assemblage zones, in ascending order: *Foerstephyllum-Billingsaria*-\**Stratodictyon*; *Hillophyllum-Tetradium*-\**Rosenella*; *Propora*-\**Ecclimadictyon-Cliefdenella*; and *Favistina-Halysites-Plasmoporella* (asterisks denote the stromatoporoids). These assemblage zones have not been applied outside central NSW, though generalized correlations between the informally numbered NSW faunal assemblages and the Tasmanian associations (see below) have been previously made (see WEBBY, 1979b; WEBBY in WEBBY & others, 1981, p. 9–10; WEBBY, 1991; WEBBY in YOUNG & LAURIE, 1996, p. 83–84). The two lower coral-sponge assemblage zones span Australasian regional stages from Gisbornian (=global Sandbian Stage)

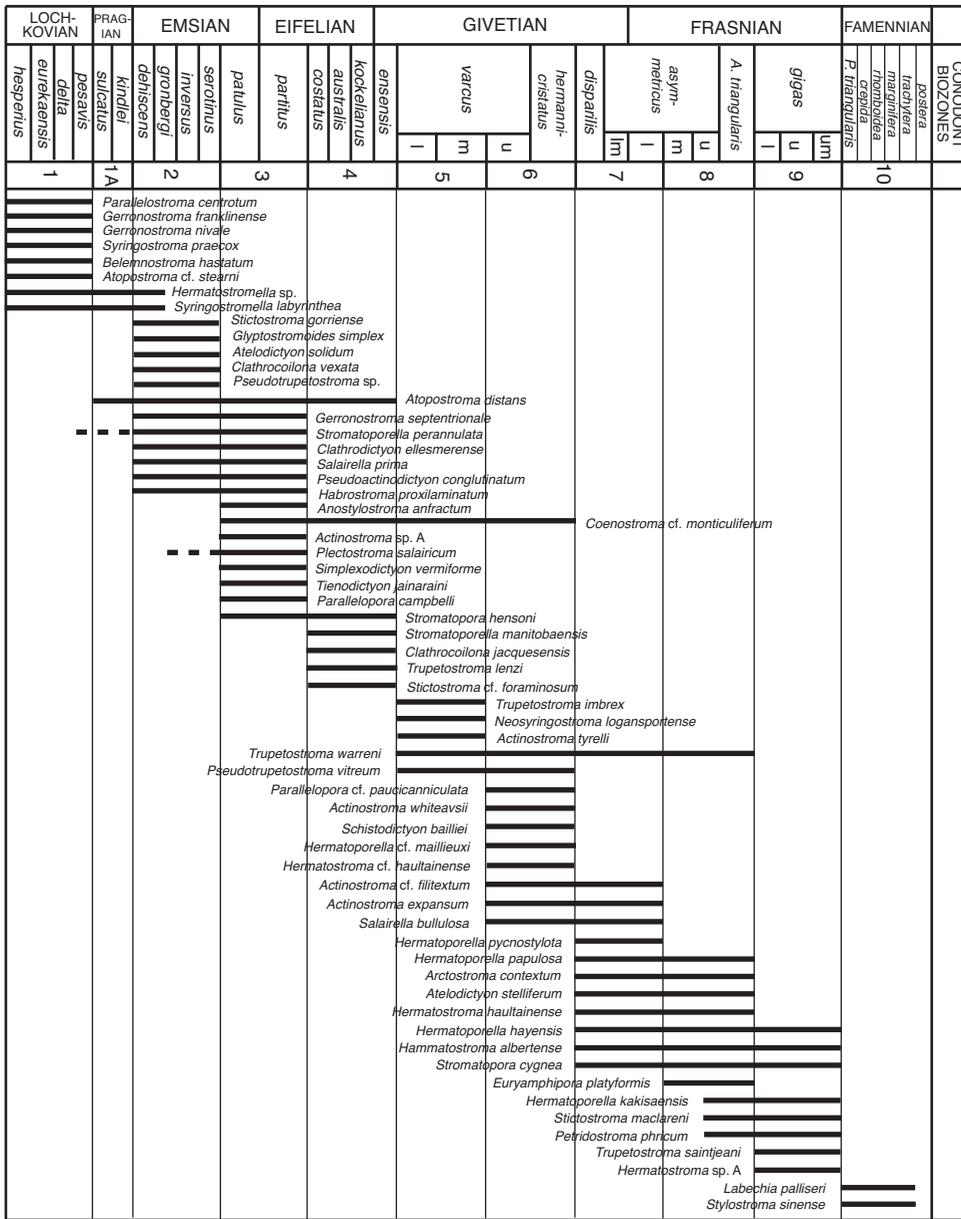


FIG. 366. Diagram depicting stratigraphic ranges of diagnostic stromatoporoid species that form the basis for establishment of ten stromatoporoid assemblage zones through Devonian successions of Arctic and Western Canada by Stearn (2001), and ties to the standardized conodont zonation of Klapper and Ziegler (1979), Klapper and Johnson (1980), Orchard (1989), and Uyeno (1990, 1991).

to lowermost Eastonian, and the two upper zones range between the middle and upper Eastonian. These latter three Eastonian zones equate with lower-middle parts of the

global Katian Stage (WEBBY & others, 2004; BERGSTRÖM & others, 2006).

Stromatoporoids are important constituents of the Ordovician carbonate succession

(Gordon Group) on the Tasmanian Shelf (WEBBY, 1979b, 1991). The two lower faunal assemblages exhibit abundant and varied labechiids, and similarly span the Gisbornian and lower part of the Eastonian, and the two upper assemblages, composed of labechiids and abundant clathrodictyids, have a mid-late Eastonian age. A general similarity exists in the stromatoporoid successional patterns of the Tasmanian Shelf and offshore NSW island arc, but few species are common to the stromatoporoid assemblages of the two regions (WEBBY in WEBBY & others, 2000).

KAPP and STEARN (1975) recognized three assemblage zones through the Day Point and Crown Point formations of the Chazy Group of Vermont (eastern North America) that effectively outline the rapid initial evolutionary expansion of the oldest indubitable reef-forming labechiid stromatoporoids during late Mid-Ordovician (late Darriwilian) time. Zone I of the upper Day Point to basal part of the Crown Point Formation contains only *Pseudostylodictyon lamottense*. The base of Zone II is characterized by appearances of the genera *Labechia* and *Pachystylostroma* (a total of five species) within the lower Crown Point. A further stage of diversification of *Pachystylostroma*, and the appearance of *Stratodictyon*, marked the succeeding Zone III, which spanned from the middle Crown Point through the Valcour Formation. WEBBY (1979b, p. 240) noted that, although the main expansion of the Labechiida in North America and Tasmania appeared to be “strikingly rapid,” the earliest part of the initial diversification in the Day Point and lower Crown Point formations of the Chazy Group apparently preceded the appearance of the earliest Tasmanian assemblage, in the Cashion Creek Limestone of Gisbornian age (WEBBY, 1991).

BOLTON (1988) recorded the stratigraphic distribution of Ordovician stromatoporoid species across central and eastern Canada. His discoveries of new records of *Ecclimadictyon* established that the clathrodictyid

stromatoporoids made their first appearances in North America during the Edenian; in global terms, early Katian (=Australasian mid-Eastonian, or British late Caradoc), as the group first appeared in Australia, northern China (LIN & WEBBY, 1988), and in Baltoscandia.

STEARNS (1997b) outlined the main Silurian faunal assemblages represented in Canadian rocks at the generic level. He distinguished five assemblages and listed their distinguishing genera: (1) early Llandovery; (2) late Llandovery (Telychian); (3) Wenlock; (4) Ludlow; and (5) Pridoli. These faunas were cross referenced to a large correlation chart for the whole country.

## DEVONIAN

Although stratigraphic position of Devonian stromatoporoids was indicated for species described in the first half of the twentieth century, no synthesis of stratigraphic ranges into a biostratigraphic scheme was attempted. LECOMPTÉ (1951 in 1951–1952) did not attempt any zonation or correlation of the Devonian species data from the Ardennes, but he found that about half of the species he distinguished were confined to one of the five intervals of stage (Givetian) or half-stage durations (Couvinian 1 & 2, Frasnian 1 & 2). The first paper written specifically on the biostratigraphy of stromatoporoids is that of FLÜGEL (1962). He considered that the group had a potential for use in stratigraphy after reviewing the distribution of the major faunas that had been described until that time. In a subsequent review of the whole group (FLÜGEL, 1975), he did not include a section on biostratigraphy but emphasized paleobiogeography and paleoecology.

Starting in the 1950s, ZUKALOVA documented the stratigraphic distribution of stromatoporoids in the Givetian and Frasnian from the Moravian Karst, Czech Republic (1958, 1974). In 1971, she described the taxonomy of all the stromatoporoid species

and recorded the ranges of all the 66 species of stromatoporoids (ZUKALOVA, 1971, table 7). Later, the Givetian to Famennian stromatoporoid succession was divided into 7 biozones (GALLE & others, 1988), and the ranges of the stromatoporoids in Moravia were plotted and keyed to conodont zones, but no attempt was made to apply this zonation to correlation problems beyond the Czech Republic.

STEARNS (1975b) attempted to divide a local section on Mount Haultain in the Rocky Mountains of Alberta into vertically successive assemblages on the basis of the overlapping ranges of stromatoporoid species. He interpreted these assemblages largely in terms of changing conditions on the reef front, but he also suggested that two zones, those of *Stromatopora parksi* and *Stictostroma mclareni*, could be useful for regional correlation.

For a 1979 review, STEARNS compiled the stratigraphic position of Devonian species and used these to plot the ranges of Devonian genera. He distinguished three major faunal intervals. The Gedinian to Emsian faunal interval was characterized by forms transitional from the Silurian, the Eifelian to Frasnian interval by the maximum stromatoporoid diversity, and the Famennian to Strunian interval by the return of the labechiids, and particularly *Stylostroma*. The Strunian, since ICS-IUGS ratification of the Devonian-Carboniferous boundary in 1990, has been adopted as the uppermost part of the Famennian (OLIVER & CHLUPAC, 1991; OGG, 2004).

LESSOVAYA (in KIM & others, 1978; LESSOVAYA, 1984) delineated in detail the ranges of Lower and Middle Devonian stromatoporoids in Uzbekistan and adjacent areas. She plotted the ranges of species across the boundary between these series. Also, LESSOVAYA (1982) distinguished the characteristic stromatoporoid assemblages of the Lochkovian, Pragian, and Kitabian (=Emsian) stages in the southern Tian Shan.

MISTIAEN (1999), MISTIAEN and GHOLAMALIAN (2000), and MISTIAEN (in BRICE,

MISTIAEN, and ROHART, 1999) have demonstrated that the Devonian stromatoporoid species from the Kerman and Chahrisheh regions of central Iran are closely similar to Frasnian assemblages in Afghanistan (five out of the eight species in common), as well as to assemblages in Old World regions of Europe; for example, with ties based on three species in common to the *Syringostromella? cooperi* Zone of the Boulonnais area of northern France (MISTIAEN, 1988; MISTIAEN in BRICE, MISTIAEN, & ROHART, 1999).

In the Devonian of the Michigan Basin, FAGERSTROM (1982, p. 64) identified three local stromatoporoid assemblage zones, named after relatively common species; in ascending order, *Anostylostroma columnare*, *Syringostroma sherzeri*, and *Amphipora nattresi*, but they were considered to be of little value for regional correlations.

COCKBAIN (1984) outlined a threefold assemblage zonal scheme for the Middle to Upper Devonian Canning Basin reef complexes of Western Australia, which comprise the *Anostylostroma ponderosum*–*Stromatopora cooperi* and the *Stachyodes costulata*–*Clathrocoilona spissa* zones. They are characteristic of the Sadler and Pillara limestones respectively (spanning from near the Givetian-Frasnian boundary into the Frasnian), and the overlying *Clathrocoilona saginata*–*Stromatopora lennardensis* Zone of the Windjana Limestone (Famennian). The *Stachyodes costulata*–*Clathrocoilona spissa* Zone has also been identified in the Gneudna Formation of the Carnarvon Basin (COCKBAIN, 1985) some 1200 km away, suggesting that this zonal scheme may have some potential for wider, intracontinental correlation. Note that *Syringostromella? cooperi* LECOMPTE, 1952 (in LECOMPTE, 1951–1952), recognized in northern France (see two previous paragraphs, above), and *Stromatopora cooperi* LECOMPTE, 1952 (in LECOMPTE, 1951–1952) in the Canning Basin, represent the same species and zonal index. It is remarkable therefore that this

same species, either singly or coupled with another zonal indicator species, is available within a part of the Frasnian for use in even wider-range, intercontinental correlation, such as between northern Europe and Western Australia.

KREBEDÜNKEL (1995) has published detailed logs of outcrop sections in the Gladbach-Paffrath basin of western Germany, which include the listing of stromatoporoid species found in each bed. A chart (1995, fig. 12) showed the ranges of the species he identified in the Givetian and Frasnian strata. Plotted on

another chart (1995, fig. 20) were the occurrences of species common to Europe, Russia, North America, Asia (China), and Australia.

BOGOYAVLENSKAYA (2001b) summarized the occurrence of stromatoporoids on the Russian Platform in terms of the Devonian conodont zonation. She also illustrated the changes in diversity of these faunas throughout the Devonian; by far, the most diverse faunas are of Frasnian age. No attempt was made to establish stromatoporoid-based zones or to use stromatoporoid ranges for correlation.