

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 CO₂, 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,

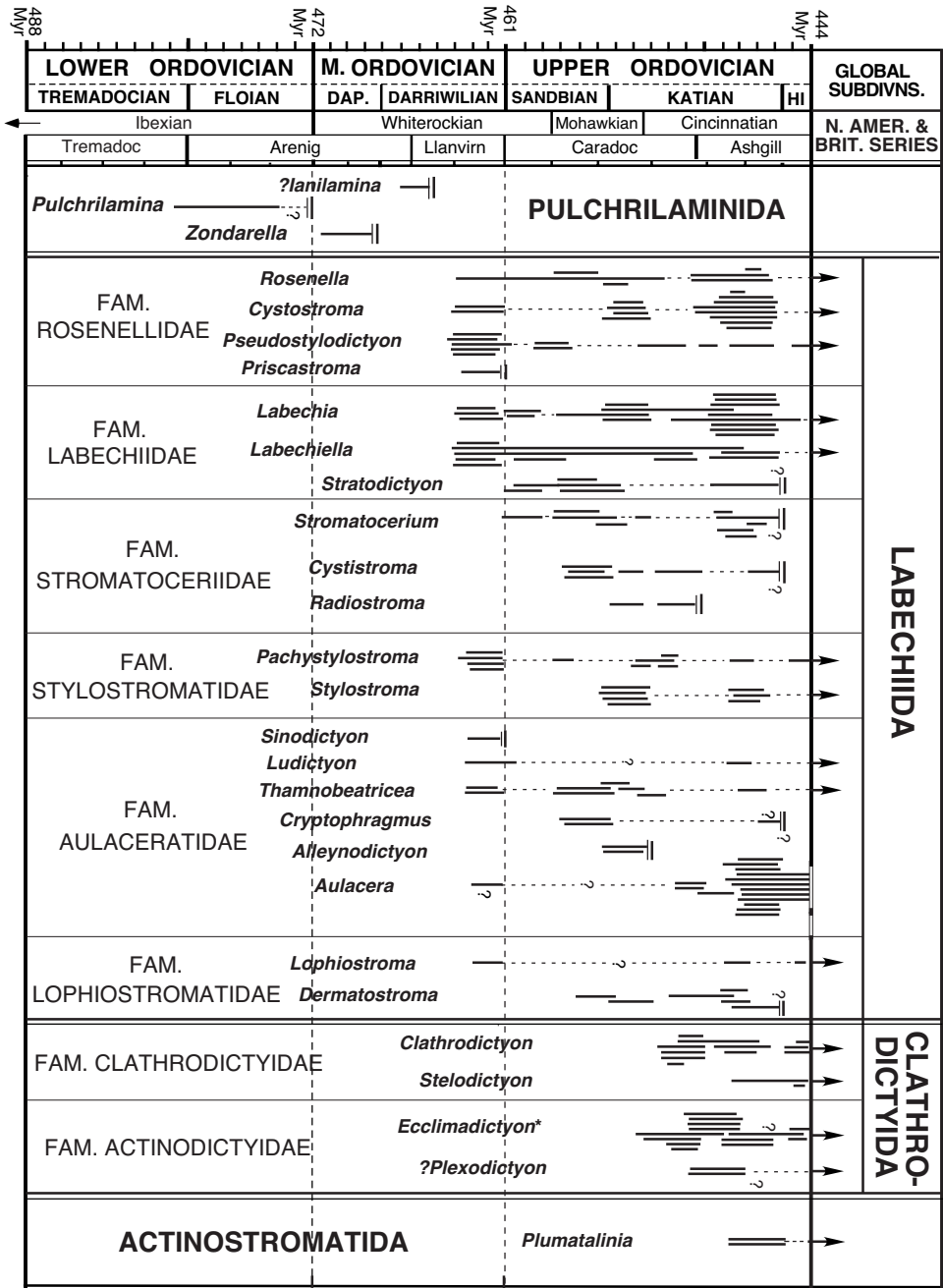


FIG. 358. (For explanation, see facing page).

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 Darrwilian 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 Darrwilian 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 Darrwilian 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).

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 *Pseudostylodictyon* (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, *Pseudostylocydon* OZAKI, 1938, was subdivided into two genera (*Pseudostylocydon* 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 *Pseudostylocydon*. 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

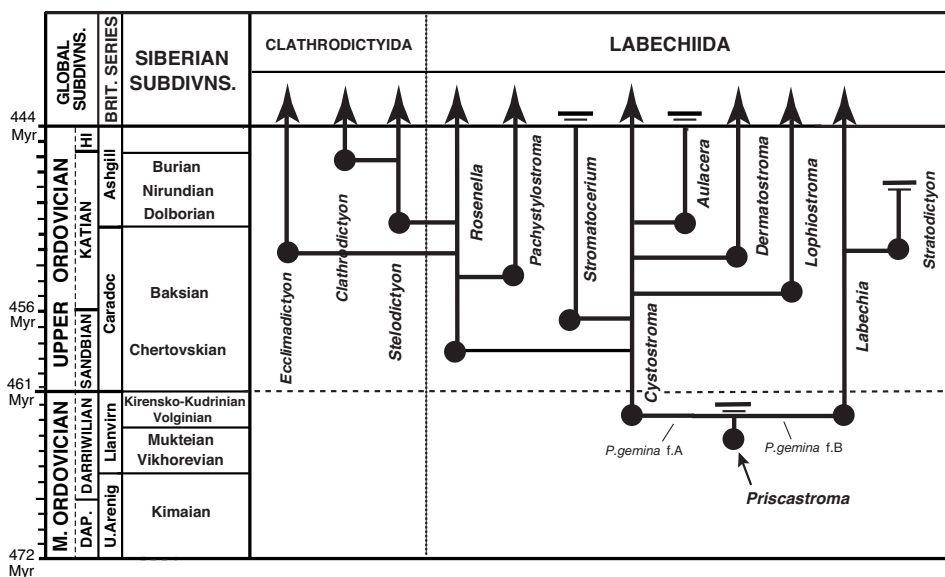


FIG. 359. Chart showing the inferred evolutionary relationships of 13 Mid–Late Ordovician stromatoporoid genera (10 labechiids, 3 clathrodictyids) from the Siberian Platform and Taymyr Peninsula (northeastern Siberia), based on data assembled by KHROMYKH (2010). The ranges of individual genera are shown 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 *Stromatocarium* (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 Chazyan 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 *Pseudostyloclycyon* 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).