

TREATISE ONLINE

Number 9

Part E, Revised, Volume 4, Chapter 11A:
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Paleozoic Stromatoporoidea

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2010

KU PALEONTOLOGICAL
INSTITUTE

The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART E, REVISED, VOLUME 4, CHAPTER 11A: DIVERSITY TRENDS OF THE PALEOZOIC STROMATOPOROIDEA

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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 *Treatise Online*, Part E, Revised, Volume 4, Chapter 16A–16B) are the bases of this chapter (Fig. 1–2). Studies of diversity trends in the stromatoporoids have been published by NESTOR and STOCK (2001), COPPER (2002), WEBBY (2004), and STOCK (2006). COPPER's (2002) diagram, which closely resembles Figure 1, was compiled from the review of stromatoporoid 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 *Treatise Online*, Part E, Revised, Volume 4, Chapter 12, Fig. 1). 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

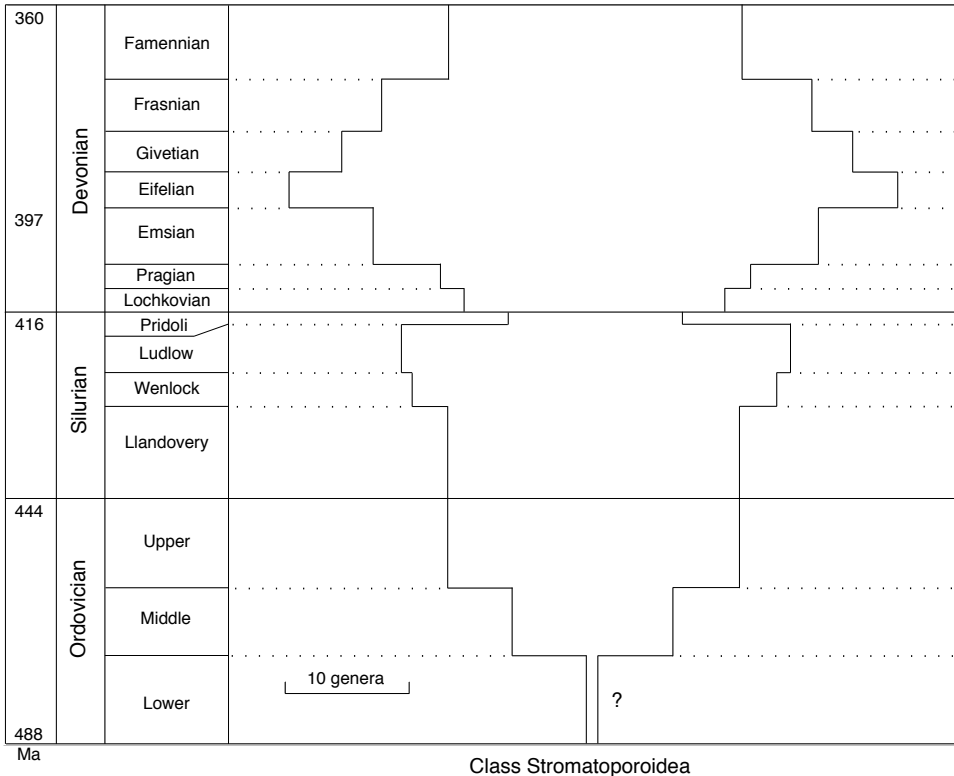


FIG. 1. Generic diversity of the class Stomatoporoidea. The vertical intervals are proportional to their time value in the geologic time scale. Ages in millions of years (Ma) are indicated on the left; question mark in the Lower Ordovician denotes the author's view that the Pulchrilaminida is doubtfully ancestral to the class Stomatoporoidea. According to WEBBY (*Treatise Online*, Part E, Revised, Volume 4, Chapters 10 and 17), however, the new order Pulchrilaminida lacks close links to the Stomatoporoidea and, consequently, is best considered a completely independent hypercalcified sponge group of the class Uncertain (new; time scale according to Gradstein, Ogg, & Smith, 2004).

stromatoporoid orders rather than the exact number of genera in each time slice. The time scale used in calculations for Figure 1 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 chapters on Evolution and Extinction (see *Treatise Online*, Part E, Revised, Volume 4, Chapters 10 and 11B). 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.

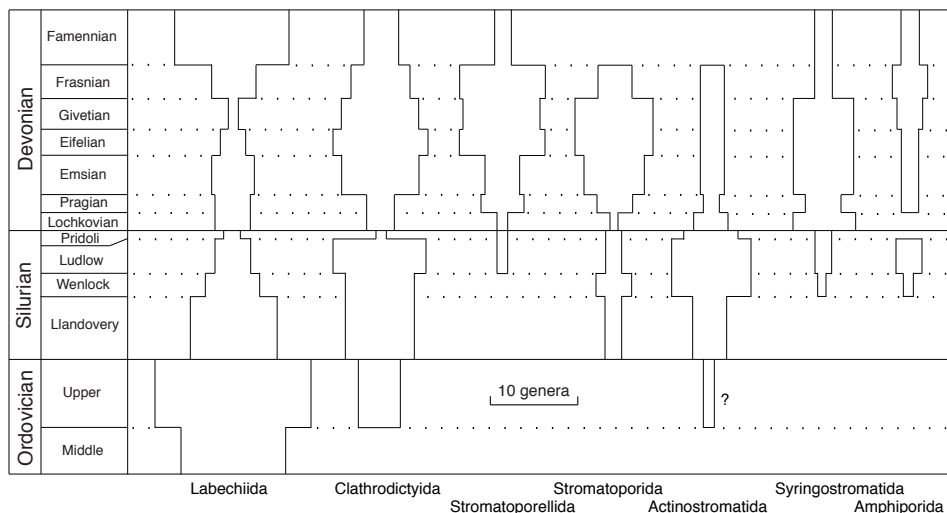


Fig. 2. Generic diversity of the orders of the class Stromatoporoida, with the exception of the Pulchrilaminida. Time scale as in Figure 1. The extension of the Actinostromatida into the Upper Ordovician is based on the opinion of STOCK and NESTOR (personal communication, 2006) that the genus *Plumatalinia* is an actinostromatid, but WEBBY (see *Treatise Online*, Part E, Revised, Volume 4, Chapter 10), 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 (new; time scale according to Gradstein, Ogg, & Smith, 2004).

2) 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. 1). 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 chapter on Extinction Patterns (see *Treatise Online*, Part E, Revised, Volume 4, Chapter 11B).

The greatest diversity of the class as a whole occurred in the middle of the periods (Fig. 1). 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 chapter on Extinction Patterns, *Treatise Online*, Part E, Revised, Volume 4, Chapter 11B) 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. 2). 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, 2004), although a problematical *Zondarella*-like taxon named *Ianilamina* PICKETT & ZHEN (in ZHEN & PICKETT, 1998), which was found recently in the early Darriwilian of New South Wales, largely 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, 2004). 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 *Eclimadictyon*, 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 stromatoporids 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 2 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

2 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.

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