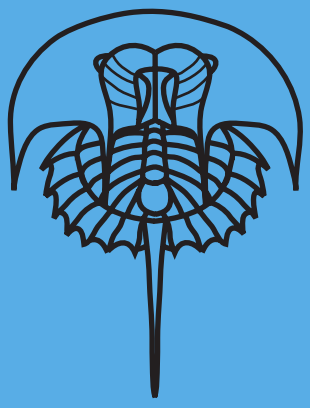

TREATISE ONLINE

Number 12

Part E, Revised, Volume 4, Chapter 15B: Classification of the 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 15B: CLASSIFICATION OF THE PALEOZOIC STROMATOPOROIDEA

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INTRODUCTION

The Paleozoic stromatoporoids have been considered, among other groups, to be an order of the class Hydrozoa (e.g., NICHOLSON, 1886; LECOMPTE, 1956; BOGOYAVLENSKAYA, 1969, 1984), a subphylum of the phylum Porifera (e.g., STEARN, 1972), and a class of the Porifera (e.g., STEARN & others, 1999; and *Treatise Online,* Part E, Revised, Volume 4, Chapter 16). Recently, the most commonly adopted rank for this group has been a class of the Porifera.

BASIS OF CLASSIFICATION

In sorting or classifying fossils, the paleontologist decides which of the features of morphology or life history of the group are important, and which are trivial. An important influence on classification has been the living group to which the fossil group has been assigned. Although the first writers describing the stromatoporoids suggested they were sponges (see Morphologic Affinities, *Treatise Online,* Part E, Revised, Volume 4, Chapter 9E), the consensus from the 1870s to the 1970s was that they were Hydrozoa and that the morphology of that living group should be the guide to assessing the relative importance of features of the fossil for classification. Thus NICHOLSON's classification (1886), which was followed for a century by many writers, was based on the division of the fossils of the four families into groups that resembled the living hydroids *Hydractinia* (Hydractinoidea) and those that resembled *Millepora* (Milleporoidea). Comparison with these living hydroids also influenced the classification used by LECOMPTE (1956) in volume F of the *Treatise on Invertebrate Paleontology* and KÜHN (1939). TRIPP (1929) and BOGOYAVLENSKAYA (1984) made detailed comparisons between living hydroids and fossil stromatoporoids.

The selection of a single morphological feature as the basis for classification has appealed to several paleontologists. HEINRICH (1914) divided stromatoporoids into families in which the microstructure was homogeneous (Actinostromatidae) and in which it was porous or tubular (Stromatoporidae). The sensitivity of the skeleton to diagenesis has discouraged other writers from reliance on microstructure for classification (LECOMPTE, 1956; STEARN, 1966). BOGOYAVLENSKAYA (1965, 1969) proposed that the form of the astrorhizae should be the basis of major divisions of the stromatoporoids, but she did not use this criterion in practice. Other classification schemes have been based on the overall morphological similarity of the groups rather than a single feature. STEARN (1980, p. 880–881) called such schemes phenetic and explained that in them the higher taxonomic groups (for instance, orders) ". . . are conceived as being groupings of lower taxa (e.g., families) which share more morphological features in common than they share with taxa (other families) of another higher taxon (another order)." While it is easy to formulate diagnoses for higher taxa distinguished by single or few distinguishing features, it may be difficult to diagnose higher taxa based on overall similarity.

The methods grouped as cladistics depend on a compilation of a series of

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Stearn, C. W. 2010. Part E, Revised, Volume 4, Chapter 15B: Classification of the Paleozoic Stromatoporoidea. Treatise Online 12:1–9.

character states that together express overall similarity and comparison of these states to an outgroup. For the stromatoporoids, cladistics has been applied only to the labechiids. WEBBY (1994) used 16 derived characters to produce a cladogram and division of the order into 4 families. The small number of morphological features of the stromatoporoids that can be factored into cladistic analysis appears to have limited the further application of this methodology.

The ideal classification will faithfully reflect the phylogeny of the Paleozoic stromatoporoids. Ideally each higher taxon should be monophyletic, that is, derived from a single ancestor. Many taxonomists assume that overall similarity of morphology is a reliable guide to ancestry (like begets like). Textbooks discuss exceptions to this principle caused by convergent evolution. STEARN's (1993, fig. 4) revision of the order Stromatoporida is an example of a classification based on overall similarity as a guide to a reconstructed phylogeny.

TREATISE CLASSIFICATION

The classification used in this volume has been slightly modified from that published by STEARN and others (1999). The main changes in higher taxa from that classification are as follows.

1. Addition of the family Platiferostromatidae.

2. Deletion of the subfamilies Pseudolabechiinae and Plumataliniinae from the family Pseudolabechiidae.

3. Substitution of the name Coenostromatidae for Syringostromatidae in the order Syringostromatida.

4. Introduction of a new family to the Clathrodictyida: the Anostylostromatidae.

The classification is based on the overall similarity of structural elements in the skeletons but emphasizes microstructures of these elements and phylogeny of the taxa. The authors assume and hope that the major groups are monophyletic, but monophyly is difficult to prove.

Phylum Porifera GRANT, 1836
- Class Stromatoporoidea NICHOLSON & MURIE, 1878
  - Order Labechiida KÜHN, 1927
    - Family Rosenellidae
    - Family Labechiidae
    - Family Stromatoceriidae
    - Family Platiferostromatidae
    - Family Stylostromatidae
    - Family Aulaceratidae
    - Family Lophiostromatidae
  - Order Clathrodictyida BOGOYAVLENSKAYA, 1969
    - Family Clathrodictyidae
    - Family Actinodictyidae
    - Family Gerronostromatidae
    - Family Tienodictyidae
    - Family Anostylostromatidae
    - Family Atelodictyidae
  - Order Actinostromatida BOGOYAVLENSKAYA, 1969
    - Family Actinostromatidae
    - Family Pseudolabechiidae
    - Family Actinostromellidae
    - Family Densastromatidae
  - Order Stromatoporellida STEARN, 1980
    - Family Stromatoporellidae
    - Family Trupetostromatidae
    - Family Idiostromatidae
  - Order Stromatoporida STEARN, 1980
    - Family Stromatoporidae
    - Family Ferestromatoporidae
    - Family Syringostromellidae
  - Order Syringostromatida BOGOYAVLENSKAYA, 1969
    - Family Coenostromatidae
    - Family Parallelostromatidae
    - Family Stachyoditidae
  - Order Amphiporida RUKHIN, 1938
    - Family Amphiporidae
  - Order and Family Uncertain
- Class Uncertain
  - Order Pulchrilaminida WEBBY, new
    - Family Pulchrilaminidae

Seven of the formally named orders unite stromatoporoids of similar, but not unique, skeletal architecture and microstructure that can reasonably be considered to be a clade. The

labechiids are characterized by an architecture based on cyst plates but include forms that also incorporate laminae and pillars. Their early appearance in the Middle Ordovician and the persistence of conservative morphologies in the order to the end of the Devonian suggest that they are the basic stock from which the other orders evolved. In the Late Ordovician, they grade into the actinostromatids, whose skeletal network is based on pillars of a range of sizes giving off colliculi to form lacy laminae. The clathrodictyids appeared after the labechiids in early Late Ordovician time, possibly from noncalcified ancestors, and built skeletons of single-layer, compact laminae, combined with a wide variety of pillars that spanned the spaces between them. The stromatoporellids had laminae that are more complex, typically thick and divided into layers. STEARN and PICKETT (1994) suggested that they, and the clathrodictyids, may have formed their skeleton in modules like that of the sponges informally grouped as sphinctozoans. The stromatoporids arose at the end of early Silurian time, probably from clathrodictyid ancestors, and were characterized by amalgamate skeletons formed of pachysteles and pachystromes of cellular microstructure. *Eostromatopora*, which is of obscure microstructure, may have been an ancestor. Structural elements with cellules are not confined to the stromatoporids, however; elements of similar microstructure also occur in the stromatoporellids. The syringostromatids are typically a Devonian group but are believed to have evolved in middle Silurian time from the actinostromatids. They built skeletons of pachysteles, pachystromes, and columns typically of microreticulate microstructure. NESTOR and STOCK (personal communication, 2006) are of the opinion that the order Syringostromatida should be divided into an order with clinoreticular microstructure derived from the Pseudolabechiidae and an order with orthoreticular microstructure derived from the Actinostromellidae or Densastromatidae. The amphiporids are a small group of abundant fossils, most of which are digitate, columnar, or dendritic in form, and composed of a network of compact, fibrous, or vacuolate elements. The order Pulchrilaminida is a small, independent, Early to Mid-Ordovician group of hypercalcified sponges assigned to class Uncertain (see *Treatise Online,* Part E, Revised, Volume 4, Chapters 10 and 17).

HISTORICAL REVIEW
1826–1980

The classifications of Paleozoic stromatoporoids published before 1980 have been reviewed by LECOMPTE (1956) and STEARN (1980); no purpose would be served by repeating these summaries of older work. Few papers have been published that cover the whole class and provide diagnoses of each higher taxon. The literature on classification since 1980 will be discussed in the following section.

LECOMPTE's (1956) critiques of previous viewpoints on classification were based on his convictions that: (1) the stromatoporoids were hydroids; (2) microstructures were of little value in their classification; and (3) the Mesozoic stromatoporoid-like forms should be integrated into the families of Paleozoic stromatoporoids. None of these convictions are held by the writers of this section of the volume (see *Treatise Online,* Part E, Revised, Volume 4, Chapters 9A–16E). He outlined the classifications used by NICHOLSON (1886), HEINRICH (1914), DEHORNE (1920), STEINER (1932), and KÜHN (1939) before proposing a new classification of 10 families (plus an uncertain group). He also included in the stromatoporoids the Cambrian forms (YAVORSKY, 1932) of the former Soviet Union that have generally been excluded from the Stromatoporoidea by most specialists (e.g., NESTOR, 1966). LECOMPTE's classification was criticized (ST. JEAN, 1957) and then largely ignored by paleontologists. Its neglect was partly owing to the publication soon after of GALLOWAY's 1957 classification, which proved more acceptable to those working with this group, including YANG and DONG (1962), who used it in their first comprehensive survey of Chinese stromatoporoids. YAVORSKY, who contributed five major monographs on stromatoporoids of the former Soviet Union through the 1950s and 1960s,

also found it difficult to use LECOMPTE's classification, preferring to use a simpler scheme for the Paleozoic forms (YAVORSKY, 1962) based on NICHOLSON's four original families: Actinostromatidae, Labechiidae, Stromatoporidae, and Idiostromatidae.

STEARN (1980) also briefly reviewed the history of classification of the Paleozoic stromatoporoids from the beginning and proposed a modification of the GALLOWAY (1957) classification to include the many new genera proposed from the Soviet Union. His classification was based on overall similarity and minimized the influence of microstructures in defining higher taxa. Major modifications of STEARN's (1980) classification made in this *Treatise* involve the giving of a larger place to microstructure in the criteria of classification, as well as the following modifications.

1. Splitting off of the Stylostromatidae and Stromatoceriidae from the Labechiidae.

2. Removing the Lophiostromatida as an order to a family of the Labechiida.

3. Removal of the Ecclimadictyidae as a family and placing some of these genera in the family Actinodictyidae.

4. Recognition of the families Gerronostromatidae, Atelodictyidae, and Anostylostromatidae in the Clathrodictyida.

5. Removal of the Syringostromatidae from the Stromatoporida to a separate order with new families Coenostromatidae, Parallelostromatidae, and Stachyoditidae.

6. Recognition of the amphiporids as a separate order and removal from the Clathrodictyida.

1980–2009

An extensive analysis of stromatoporoid morphology, interpretation, and classification from a Soviet Union perspective was published in 1984 by BOGOYAVLENSKAYA, based on earlier papers (BOGOYAVLENSKAYA, 1969, 1974). This was followed in 1985 by a catalogue of genera and species of the stromatoporoids by BOGOYAVLENSKAYA and KHROMYKH. BOGOYAVLENSKAYA compared the classifications of NICHOLSON (1886), KÜHN (1939), LECOMPTE (1956), GALLOWAY (1957), and KHALFINA and YAVORSKY (1973) in a table. BOGOYAVLENSKAYA's own classifcation reflected her belief that the stromatoporoids were hydrozoans and that the Mesozoic stromatoporoid-like fossils should be included in the subclass. Her classification of 1984 did not include Mesozoic genera, however. She formulated a phylogeny diagram showing an interpretation of the relationship between the taxa. The following is a summary of her higher taxa.

Subclass Stromatoporata
- Order Labechiida
  - Family Aulaceratidae
  - Family Stratodictyidae
  - Family Tuvaechiidae
  - Family Labechiidae
  - Family Stromatoceriidae
- Order Clathrodictyida
  - Family Clathrodictyidae
  - Family Plexodictyidae
  - Family Actinodictyidae
  - Family Stromatoporellidae
  - Family Coenellostromatidae
- Order Actinostromatida
  - Family Plumataliniidae
  - Family Pseudolabechiidae
  - Family Densastromatidae
  - Family Actinostromatidae
  - Family Atelodictyidae
- Order Gerronostromatida
  - Family Gerronostromatidae
  - Family Simplexodictyidae
  - Family Tienodictyidae
- Order Syringostromatida
  - Family Parallelostromatidae
  - Family Clathrocoilonidae
  - Family Pichiostromatidae
  - Family Syringostromatidae
  - Family Hermatostromatidae
- Order Stromatoporida
  - Family Stromatoporidae
  - Family Ferestromatoporidae
- Order Incertae Sedis
  - Family Cleifdenellidae [*sic*]
  - Family Amphiporidae
  - Family Lophiostromatidae

As might be expected, many of BOGOYAVLENSKAYA's higher taxa are recognized in

the classification adopted here. The major changes for the *Treatise* classification are as follows.

1. Removal of the Tuvaechiidae as a separate family.

2. Recognition of the Stromatoporellida as a separate order, not a family.

3. Placing of the Gerronostromatida as a family in the Clathrodictyida.

4. Placing of the Simplexodictydae in the Stromatoporellida, with the exception of *Anostylostroma,* which is a clathrodictyid.

5. Reinterpretation of the Syringostromatida based on the typical genus and removal of the genera grouped in the Clathrocoilonidae and Hermatostromatidae to the Stromatoporellida.

6. Assignment of the genus *Pichiostroma* to the Actinostromellidae and removal of the family.

7. Removal of the Cliefdenellidae from the Stromatoporoidea (Webby & Lin, 1988).

8. Recognition of the Amphiporida as a separate order.

9. Assignment of the Lophiostromatidae to the Labechiida.

Bogoyavlenskaya and Lobanov (1990) reviewed the morphological relationships, phylogeny, and paleogeography of many genera of the labechiids. They proposed another family be established in this order, the Cystostromatidae, to include the genera *Cystostroma* and *Pachystylostroma.*

Webby (1979, 1986, 1993) has written extensively on the early history of the stromatoporoids and the classification and phylogeny of the labechiids. In 1979, he reviewed the genera of the labechiids and clathrodictyids that accompany them in Ordovician rocks and the speculations of Galloway (1957), Nestor (1966), Bogoyavlenskaya (1969), and Kazmierczak (1971) that the former gave rise to the latter in Mid–Late Ordovician (Katian) time. Herein, the labechiiids were considered to be an undivided family. In 1986, Webby recognized a division of the labechiids into the Rosenellidae, Aulaceridae, Lophiostromatidae, and Labechiidae and speculated on the origin of the group from *Pulchrilamina* (which he included in the Labechiidae) and part of the Cambrian Khasaktiidae, which he included in the Stromatoporoidea (Webby, 1986, fig. 10). By 1993, Webby had increased the number of families in the order Labechida to six with the addition of the Pulchrilaminidae (doubtfully assigned) and the Stylostromatidae (Webby, 1993, 1994). Webby's evolving views on the classification of the labechiids are recorded by his doubtful inclusion of the pulchrilaminids in the labechiids (Stearn & others, 1999) and his later exclusion of them from the order to an indeterminate position (Webby, 2004). They are now separated in this *Treatise* volume into a small, independent order of hypercalcified sponges of stromatoporoid-like appearance with uncertain phylogenetic relationships. Nestor (in Stearn & others, 1999, p. 60) regarded two of the khasaktid genera as being possibly parts of archaeocyath holdfasts. In this volume, the Khasaktidae are removed entirely from an association with the stromatoporoids (see comments in discussion of class Stromatoporoidea, *Treatise Online,* Part E, Revised, Volume 4, Chapter 16A). Webby (1994, p. 379) noted that the morphological gradations between first-appearing clathrodictyid (Late Ordovician) genera—*Clathrodictyon* on the one hand and *Ecclimadictyon* and *Plexodictyon* on the other—do not support the differentiation of these genera into separate families during their early developmental history. Webby, Stearn, and Zhen (1993) used the classification of Stearn (1980) in their description of non-labechiid Lower Devonian stromatoporoids from the state of Victoria, Australia.

The Chinese viewpoint on classification has been formulated largely by Dong De-yuan, who wrote numerous reports on Chinese Paleozoic stromatoporoids during the 1980s and 1990s. In 1983, he recognized nine different pillar microstructures and described the form of pillars of many genera. In 1987, Dong presented an extensive summary of the group, including

sections on the significance of morphologic features, microstructures, and principles of classification. This handbook reviewed the classification of NICHOLSON (1886), KÜHN (1927), LECOMPTE (1956), GALLOWAY (1957), BOGOYAVLENSKAYA (1965, 1969), and KHALFINA and YAVORSKY (1973). DONG's (1987) classification is basically a modification of STEARN's (1980) classification with the following differences.

1. The family Platiferostromatidae was established within the Labechiida to receive, in most part, Famennian stromatoporoid genera from China.

2. The family Gerronostromatidae was established within the Actinostromatida to receive genera, which are regarded herein, largely on the basis of microstructure, as being of different orders (e.g., *Atopostroma* [Syringostromatida], *Amnestostroma* =*Hermatostromella* [Stromatoporellida], *Clathrostroma* = *Gerronostroma* [Clathrodictyida]).

3. The family Cubodictyonidae in the Actinostromatida was established to contain the single genus *Cubodictyon*. NESTOR (in STEARN & others, 1999) placed the genus provisionally in the Clathrodictyida (family Atelodictyidae) and suggests it may not be a stromatoporoid.

4. The new order Idiostromatida was established to accommodate three families: Idiostromatidae, Amphiporidae, and Stachyoditidae. This is an unwarranted return to the concept of NICHOLSON (1886) and GALLOWAY (1957) that digitate, columnar, and dendroid growth forms can be used as a criterion for separation of higher taxa.

The same classification was presented by DONG in 1988. The stromatoporoids were placed in the phylum Porifera, STEARN's (1980) classification was criticized, and the modifications listed above proposed. Diagnoses of the various taxa were formulated in which little significance is given to microstructure as a guide to taxonomic affinity. In DONG's (2001) monographic treatment of the stromatoporoids of China, these same higher taxa are used in the classification.

STEARN (1993) revised his classification of the order Stromatoporida by dividing it into two orders separated by microstructure and phylogeny by splitting off the Syringostromatida. The stromatoporids were postulated to have arisen from clathrodictyid or labechiid ancestors in late early Silurian time, while at a similar time, the syringostromatids evolved from actinostromatids, from which they derived their microreticulate microstructure. Only a single family was recognized in the Syringostromatida.

The section on Paleozoic stromatoporoids in *The Fossil Record 2* (RIGBY & others, 1993) is based on the classifications of LECOMPTE (1956) and STEARN (1980) and does not introduce new taxa.

In 1994, STOCK reviewed the origin, evolution, and classification of the Actinostromatida. The phylogeny of the order is traced from the Late Ordovician genus *Plumatalinia* through the early Silurian *Plectostroma* to its diversification in middle Silurian time. Although suggesting that not all genera fit into these divisions, he recognized only three families in the order: Pseudolabechiidae, Actinostromellidae, and Actinostromatidae.

NESTOR has published several versions of his classification of Paleozoic stromatoporoids as phylogenetic diagrams without diagnoses. In the first series of these, which appeared in 1974, the main divisions were recognized as the superfamilies Labechiacea, Clathrodictyacea, Actinostromacea, and Stromatoporacea. This classification differed from his subsequent ones, largely in the inclusion of the Stromatoporellidae and Hermatostromatidae in the clathrodictyids and the Syringostromatidae in the actinostromatids. In his monograph on the Silurian of the Moiero River, NESTOR (1976) removed the lophiostromatids to the superfamily Lophiostromatacea, recognized the Actinodictyidae and Synthetostromatidae in the clathrodictyids, and the Yavorskiinidae in the Stromatoporacea. In a diagram of

1994, NESTOR recognized the superfamilies as orders and proposed the following subdivisions of these orders.

Order Lophiostromatida
  Family Lophiostromatidae
Order Stromatoporellida
  Family Hermatostromatidae
  Family Synthetostromatidae
  Family Stromatoporelllidae
Order Clathrodictyida
  Family Clathrodictyidae
  Family Amphiporidae
  Family Tienodictyidae
  Family Ecclimadictyidae
Order Labechiida
  Family Rosenellidae
  Family Aulaceratidae
  Family Stromatoceriidae
  Family Plumataliniidae
Order Actinostromatida
  Family Pseudolabechiidae
  Family Actinostromatidae
  Family Densastromatidae
  Family Actinostromellidae
Order Stromatoporida
  Family Pseudotrupetostromatidae
  Family Yavorskiinidae
  Family Stromatoporidae

In NESTOR's 1997 paper and his contribution to the classification of the clathrodictyids in 1999 (in STEARN & others, 1999), he substituted the name Actinodictyidae for the Ecclimadictyidae, added the Gerronostromatidae and Atelodictyidae, and removed the Amphiporidae. In the classification adopted herein, he also added the new family Anostylostromatidae.

In 1996, KHROMYKH outlined his concept of the clathrodictyids, emphasizing the similarity of structural elements in various higher taxa and the necessity to maintain the uniformity in microstructure of such taxa. He reintroduced from his 1974 paper the superfamily Cystostromacea, which no other paleontologists have used, and divided it into various families, one of which, the Clathrodictyidae, is subdivided in the 1996 paper into the subfamilies Clathrodictyinae, Tienodictyinae, Ecclimadictyinae, and Actinodictyinae. Although NESTOR (1997) used the term Actinodictyidae as a substitute for the Ecclimadictyidae, KHROMYKH (1996) regarded the two groups of genera as separate entities.

In the *Systema Porifera*, no attempt was made by COOK (2002) to present a classification of the Paleozoic stromatoporoids.

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