

# Skeletonisation in the stenolaemate bryozoan orders Cryptostomata (Suborder Rhabdomesina) and Trepostomata: the role of the Bryozoan Skeletal Index (BSI) as a taxonomic character

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**ABSTRACT:** The Bryozoan Skeletal Index (BSI) is a measure of the relative proportion of skeleton to open space in stenolaemate bryozoans. Here the measure is calculated for the Families of the Suborder Rhabdomesina of the Order Cryptostomata and in the Order Trepostomata. Patterns show that in the former, the members of the Family Arthrostylidae yield lower BSI values than members of other cryptostome families, while in general the BSI values in the trepostomes are higher than those of the cryptostomes. A number of taxa are evaluated with respect to BSI as their ordinal or familial placement has varied according to different authors; these include *Coelotubulipora* and *Tebitopora*. For both, BSI values are low, suggesting that placement in the Cryptostomata is correct. However, other morphological characters indicate that the former is a trepostome and the latter a cryptostome. The genera *Nematotrypa* and *Cyclophaenopora* that had been placed in either the Arthrostylidae or the Nematotrypidae are considered and shown to likely belong in the latter family rather than the former. BSI is a measure that can be utilized with some value in systematic placement but only alongside salient and characteristic morphological data.

## 1 INTRODUCTION

The suprageneric arrangement of Paleozoic stenolaemate bryozoans now consists of a number of orders of which the Trepostomata erected by Ulrich (1882) and Cryptostomata (Vine 1884) both contain taxa that may develop erect growth forms that appear superficially similar. For a period in the mid-twentieth century, use of the Order Cryptostomata fell into abeyance and was only reestablished by Blake (1975) during revision of the *Treatise on Invertebrate Paleontology* which documented two cryptostome suborders, the Suborder Rhabdomesina and Suborder Ptilodictyina and their constituent genera (Blake 1983a, 1983b, 1983c; Karklins 1983a, 1983b).

The Bryozoan Skeletal Index (BSI) was devised as a measure of the relative proportion of skeleton

to open space in stenolaemate bryozoans (Wyse Jackson *et al.* 2020), and it is computed for bryozoans of the Order Trepostomata and Cryptostomata (Suborder Rhabdomesina). In this study the Suborder Ptilodictyina is not included as colonies comprise bifoliate branches for which BSI is difficult to compute as they grossly differ from ramose cylindrical colonies common in the Trepostomata and Rhabdomesinids. Earlier assessments have documented the pattern of BSI across the Calcium-Aragonite transition in the Mississippian (Key *et al.* 2022) and in the latitudinal distribution of these bryozoans through the Paleozoic (Reid *et al.* 2022).

The purpose of this paper is two-fold. Firstly, it ascertains whether the BSI values in trepostome and some rhabdomesine cryptostome families reveal trends within and between families and in the orders. Secondly, the paper examines some specific genera in which BSI may be helpful in providing taxonomic insights. The placement of a number of

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genera has remained problematic to the present day due to them possessing morphologies that are at least in part characteristic of either trepostomes or cryptostomes, and the emphasis placed on these morphologies for suprageneric assignment. This issue occurs in the Ordovician as well as in the Late Paleozoic and in some Triassic stenolaemates. Spjeldnaes (1984) erected the rhabdomesine Family Nematotrypidae to accommodate the new genus *Cyclophaenopora*. It was not clear as to which other genera he considered to belong to this family, that he noted showed both cryptostome and trepostome affinities. Gorjunova (1985) reassessed the family and included *Nematotrypa*, *Moyerella*, *Kielanopora* and *Clausotrypa*, although she excluded *Cyclophaenopora* which Bock (2022) lists in the Family Arthrostylidae. For the purpose of this exercise, we have assessed *Nematotrypa*, *Cyclophaenopora* and *Moyerella* and use BSI to assess whether all taxa might be better placed in the Arthrostylidae on this measure.

Gorjunova (2011) placed her new Family Coelotubuliporidae in the Trepostomata although it appeared that the constituent genera *Coelotubulipora* Yang, Hu & Xia, 1988 and *Dunaevella* Gorjunova, 2011 possessed morphological characteristics that parallel rhabdomesonid cryptostomes, an opinion advocated earlier by Morozova *et al.* (2006) when they described the species *C. rara* from the Devonian of Poland. The Triassic genus *Tebitopora* Hu, 1984 has been enigmatic and was originally assigned to the Trepostomata (Hu 1984) and retained there by Schäfer and Grant-Mackie (1998) but subsequently reassigned to the Cryptostomata (Ma *et al.* 2020; Powers & Pachut 2008, p. 364). What are the parallels in skeletal characters that have led to these taxonomic conundrums and can the computation of BSI in these taxa aid their taxonomic placement?

## 2 METHODS

The Bryozoan Skeletal Index (BSI) is a measure of the relative proportion of skeleton to open space in the outer exozonal portion of the colony (Wyse Jackson *et al.* 2020). It is derived from measures of three characters easily obtained from colonies: (1) maximum autozooeical apertural diameter at the zoarial surface or in shallow tangential section [MZD], (2) thickness of the zooecial wall between adjacent autozooeical apertures [ZWT], and (3) the thickness of the exozone [EW] (Figure 1) in the formula:

$$BSI = ((EW * ZWT)/MZD) * 100$$

The accuracy of BSI values computed from stenolaemate bryozoans may be affected by a number of morphological and taphonomic features. These are discussed in Wyse Jackson *et al.* (2020, p. 198) and include the development and

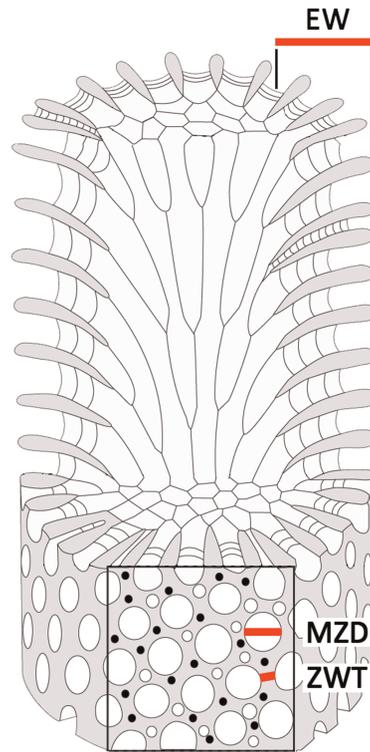


Figure 1. Morphological characters used to compute the Bryozoan Skeletal Index (BSI). From Wyse Jackson *et al.* (2020, fig. 2). Abbreviations: EW: exozone width; MZD: autozooeical aperture diameter; ZWT: autozooeical wall thickness.

positioning of maculae, inclusion of intrazooeical features, and whether ramose colonies are crushed taphonomically. In addition, where exozonal walls are moniliform and irregular in thickness as in *Stenopora* (Reid 2021), the values of MZD and ZWT may vary depending on the depth of the tangential section at which it was measured. This variation can be reduced through taking a number of measurements at different depths through the exozone, although preparation of multiple sections of peels can be time consuming, and these may not be available where literature sources are utilised. In order to provide an accurate BSI value in some globular and dome-shaped trepostome genera such as *Diplotrypa* Nicholson, 1879, recognition of the exozone-endozone boundary is required given all zooecial walls are very thin-walled unlike in most taxa in the Order.

For 83 genera of rhabdomesinid cryptostomes and 155 genera of trepostomes, the BSI was calculated from published data in type species descriptions, or from measurement of photographs of tangential and longitudinal sections except when data were published in tabular form. The age of the type species defined as the midpoint of the

type locality stratigraphic age ranges from Shanan Peters' Macrostrat.org (Key *et al.* 2022), and all numerical ages were based on the latest version of the International Chronostratigraphic Chart (Cohen *et al.* 2020). Genus stratigraphic ranges were derived from the descriptions by Boardman and Buttler (unpublished data) and augmented with Philip Bock's webpage Bryozoa.net.

BSI values were tabulated within geological periods for the type species of genera and sorted in a series of bins from low (BSI <10) to high (>200) for three groups: the arthrostyloid cryptostomes, all other rhabdomesinid cryptostomes, and the trepostomes (Table 1). To investigate ordinal and family level BSI, values were listed for the genera assigned to each Family; these familial designations follow Blake (1983c), Boardman and Buttler (unpublished data) and Taylor (1993). These BSI values were then tabulated, grouped into the same bins as in Table 1, and the total number of genera per Family is listed as are the minimum, maximum

and mean BSI values and the age range (Table 2). Families are listed in order of their first appearance at the level of stratigraphic stages from the Tremadocian (Lower Ordovician) to the Rhaetian (Late Triassic) as given in the International Chronostratigraphic Chart (Cohen *et al.* 2020). This has allowed for differences and similarities in BSI between families to be easily picked out and for trends through time to be demonstrated.

In addition to the type species used to compute the BSI for genera, additional species contained within specific taxa such as *Tebitopora* and those placed in the Family Coelotubuliporidae (*Coelotubulipora* Yang, Hu and Xia, 1988 and *Dunaevella* Gorjunova, 2011) are examined in more detail to assess whether BSI can aid taxonomic placement. BSI for the Coelotubuliporidae was computed on the basis of descriptions in original publications in which the species were first published (see listing in Table 2) and for *Tibetopora* on illustrations of the type species in Ma *et al.* (2020).

Table 1. BSI values in Cryptostome and Trepostome families. Number of genera in bins of BSI values from low (<10) to high (>200). NG = Number of Genera; X = Mean BSI; Min = Minimum BSI; Max = Maximum BSI; Age range of genera type species given in Ma. Families are listed according to their earliest appearance.

| BSI value range:     | <10 | 10–49.9 | 50–99.9 | 100–149.9 | 150–199.9 | >200 | NG         | X    | Min  | Max   | Age     |
|----------------------|-----|---------|---------|-----------|-----------|------|------------|------|------|-------|---------|
| <b>Cryptostomata</b> |     |         |         |           |           |      | <b>84</b>  |      |      |       |         |
| Arthrostyliidae      | 14  | 5       | –       | –         | –         | –    | 19         | 13.6 | 0.5  | 24    | 462–267 |
| Nematotrypidae       | –   | –       | 1       | 1         | –         | –    | 2          | 90.4 | 70.9 | 110   | 457–452 |
| Rhabdomesidae        | 4   | 17      | 6       | –         | 1         | –    | 28         | 39.6 | 3.6  | 179.4 | 425–286 |
| Hyphasporidae        | 3   | 4       | 1       | 1         | –         | –    | 9          | 35.3 | 4    | 129.2 | 403–265 |
| Rhomboporidae        | –   | 8       | 3       | –         | –         | –    | 11         | 34.8 | 10.1 | 66.1  | 399–244 |
| Nikiforovellidae     | 4   | 3       | –       | –         | –         | –    | 7          | 11.3 | 6.3  | 25.8  | 398–265 |
| Bactroporidae        | –   | 1       | –       | –         | –         | –    | 1          | 14   | –    | –     | 387     |
| Lenaporidae          | –   | 2       | –       | –         | –         | –    | 2          | 37.3 | 30.7 | 44    | 385–377 |
| Pseudoascoporidae    | 1   | –       | 1       | –         | –         | –    | 2          | 31.3 | 6    | 56.6  | 365–286 |
| Nudymiellidae        | –   | 1       | –       | –         | –         | –    | 1          | 12.3 | –    | –     | 338     |
| Goldfussitrypidae    | –   | 1       | –       | –         | –         | –    | 1          | 20   | –    | –     | 334     |
| Medvedkellidae       | –   | –       | 1       | –         | –         | –    | 1          | 60.8 | –    | –     | 305     |
| <b>Trepostomata</b>  |     |         |         |           |           |      | <b>155</b> |      |      |       |         |
| Aisenvergiidae       | –   | 4       | 3       | –         | –         | –    | 7          | 62.7 | 39   | 98    | 480–353 |
| Dittoporidae         | –   | 4       | 1       | 2         | –         | –    | 7          | 62   | 18   | 148   | 471–452 |
| Heterotrypidae       | 1   | 4       | 2       | –         | –         | –    | 7          | 35.3 | 6    | 77    | 465–243 |
| Trematoporidae       | 2   | 4       | 2       | 2         | –         | 1    | 11         | 65.4 | 4    | 200   | 464–385 |
| Ralfimartitidae      | 2   | 3       | –       | –         | –         | –    | 5          | 16   | 7    | 35    | 463–450 |
| Bimuroporidae        | 1   | 2       | –       | –         | –         | –    | 3          | 19   | 8    | 34    | 461–451 |
| Diplotrypidae        | –   | –       | –       | 1         | –         | –    | 1          | 140  | –    | –     | 461     |
| Atactotoechidae      | 4   | 5       | 4       | –         | –         | –    | 13         | 36.8 | 4    | 97    | 458–366 |
| Monticuloporidae     | –   | 3       | –       | –         | –         | –    | 3          | 16   | 12   | 18    | 456–447 |
| Mesotrypidae         | 4   | 1       | 1       | 1         | –         | –    | 7          | 30.3 | 4    | 108   | 456–449 |
| Halloporidae         | –   | 4       | –       | –         | –         | –    | 4          | 26.5 | 16   | 35    | 454–428 |
| Amplexoporidae       | –   | 7       | 1       | –         | –         | –    | 8          | 32.6 | 12   | 78    | 454–339 |
| Batostomellidae      | 1   | –       | 1       | –         | –         | –    | 2          | 38.5 | 6    | 71    | 450–449 |
| Leioclemidae         | –   | 4       | 1       | –         | –         | –    | 5          | 32   | 14   | 60    | 439–256 |

(continued)

Table 1. Continued

| BSI value range:   | <10 | 10–49.9 | 50–99.9 | 100–149.9 | 150–199.9 | >200 | NG | X    | Min  | Max | Age     |
|--------------------|-----|---------|---------|-----------|-----------|------|----|------|------|-----|---------|
| Stenoporidae       | 1   | 6       | 6       | 1         | –         | 1    | 15 | 57.3 | 7    | 211 | 432–225 |
| Hemieridotrypidae  | –   | 2       | 1       | –         | –         | –    | 3  | 45.7 | 23   | 82  | 425–421 |
| Eridotrypellidae   | 1   | 7       | 5       | –         | –         | –    | 13 | 44.2 | 7    | 94  | 425–255 |
| Anisotrypidae      | –   | 2       | 3       | –         | –         | –    | 5  | 62.4 | 28   | 86  | 419–256 |
| Stereotoechidae    | –   | 1       | –       | –         | –         | –    | 1  | 48   | –    | –   | 384     |
| Ulrichotrypellidae | –   | 2       | 1       | –         | –         | –    | 3  | 37.3 | 23   | 59  | 375–256 |
| Dyscritellidae     | –   | 5       | 1       | 1         | –         | –    | 7  | 59   | 11   | 131 | 366–232 |
| Crustoporidae      | –   | 3       | 1       | –         | 1         | –    | 5  | 51.6 | 15   | 160 | 359–305 |
| Coelotubuliporidae | 1   | 1       | –       | –         | –         | –    | 2  | 48.8 | 10.6 | 87  | 352–326 |
| Cycloporidae       | –   | 2       | –       | –         | –         | –    | 2  | 21.5 | 14   | 29  | 346     |
| Nipponstenoporidae | –   | 1       | –       | –         | –         | –    | 1  | 29   | –    | –   | 335     |
| Astralochomidae    | –   | 1       | –       | –         | –         | –    | 1  | 25   | –    | –   | 331     |
| Stenoporellidae    | –   | 2       | –       | –         | –         | –    | 2  | 30   | 12   | 48  | 328–255 |
| Mishulgellidae     | 1   | –       | –       | –         | –         | –    | 1  | 3    | –    | –   | 308     |
| Maychellinidae     | –   | 2       | 1       | –         | –         | –    | 3  | 27.3 | 13   | 56  | 274–329 |
| Araxoporidae       | –   | 3       | –       | –         | –         | –    | 3  | 29   | 18   | 35  | 260–215 |
| Zozariellidae      | –   | –       | 1       | 1         | –         | –    | 2  | 94.5 | 83   | 106 | 245–232 |

Table 2. BSI values in species of the genera *Coelotubulipora* and *Dunaevella* in the Family Coelotubuliporidae.

|  | BSI  | Geological horizon |
|--|------|--------------------|
| <i>Coelotubulipora irregularis</i> (Nekhoroshev 1956)                          | 1.3  | Devonian           |
| <i>Coelotubulipora maculata</i> (Nekhoroshev 1956)                             | 9.4  | Mississippian      |
| <i>Coelotubulipora euspinusa</i> Yang <i>et al.</i> , 1988                     | 10.6 | Mississippian      |
| <i>Coelotubulipora euspinusa ferodiaphragma</i> Yang <i>et al.</i> , 1988      | 3.3  | Mississippian      |
| <i>Coelotubulipora euspinusa clautubulosa</i> Yang <i>et al.</i> , 1988        | 13.1 | Mississippian      |
| <i>Coelotubulipora obliqua</i> Yang <i>et al.</i> , 1988                       | 7.6  | Mississippian      |
| <i>Coelotubulipora superhemisepta</i> Yang <i>et al.</i> , 1988                | 3.3  | Mississippian      |
| <i>Coelotubulipora superhemisepta clautubulosa</i> Yang <i>et al.</i> , 1988   | 2.8  | Mississippian      |
| <i>Coelotubulipora superhemisepta torquicuticula</i> Yang <i>et al.</i> , 1988 | 12.0 | Mississippian      |
| <i>Coelotubulipora interminuta</i> Yang <i>et al.</i> , 1988                   | 1.3  | Mississippian      |
| <i>Coelotubulipora bicurva</i> Yang <i>et al.</i> , 1988                       | 6    | Mississippian      |
| <i>Coelotubulipora irinae</i> Gorjunova, 2011                                  | 5    | Mississippian      |
| <i>Coelotubulipora intervacara</i> (Trizna 1958)                               | 15   | Mississippian      |
| <i>Coelotubulipora varionodata</i> (Trizna 1958)                               | 5    | Mississippian      |
| <i>Dunaevella shishovae</i> (Schulga-Nesterenko 1955)                          | 87   | Mississippian      |
| <i>Dunaevella peristomata</i> (Schulga-Nesterenko 1955)                        | 24.8 | Mississippian      |

### 3 RESULTS

BSI values calculated for 84 cryptostome and 155 trepostome genera are presented in Table 1 where values are compiled into six value bins between <10 and >200. Data by families (12 in the Order Cryptostomata and 31 in the Order Trepostomata) are provided in this table. Six trepostome genera that have not been assigned to a Family yielded BSI

values while some other trepostome families contain genera for which BSI values could not be computed either due to taphonomic preservational issues or because not all parameters were measurable, i.e., the Pseudocampylidae, Helenoporidae, Dianulitidae, Revalotrypidae and the Girtyporidae. Table 2 gives BSI values of species contained within those genera in the Family Coelotubuliporidae which have been placed at various times in either of the orders.

## 4 DISCUSSION

### 4.1 General BSI trends in cryptostome and trepostome families

The smallest most delicate cryptostomes are the arthrostylids that first appeared in the early Ordovician, but which rapidly diversified so that during this period they reached their greatest diversity. From the Devonian onwards their diversity declined, and only one genus *Pemoheloclema* Ozhgibesov, 1983 persisted into the Permian. Structurally the Arthrostylidae are varied with simple narrow erect or branched zoaria, sometimes articulated, generally with thin exozones and small stylets that may only extend marginally beyond the zoarial surface. In many taxa, autozoecial apertures are large with narrow interapertural walls. The relatively large autozoecial apertures and narrow interapertural walls lead to low BSI values within the Arthrostylidae with a mean of 13.6 (Table 1, Figure 2).

By contrast, the members of the other families in the Suborder Rhabdomesina exhibit a greater range of BSI values from 3.6 in the genus *Promediapora* Gorjunova, 1992 to 179.4 in *Muromipora* Gorjunova, 2011 that reflect their greater structural complexity (Figure 3A-B). They largely comprise erect cylindrical zoaria with a well-defined axis from which are budded short cylindrical zoecial chambers in which hemisepta or other structural elements may be developed. Apertures tend to be oval to rhombic in shape, frequently surrounded by styles of a variety of sizes

and structure, whereas interapertural areas may be skeletal or marked by the presence of space-filling metapores, especially in the Family Hyphasmoporidae. *Muromipora* has a very wide exozone comprised of thickened interapertural walls with narrow rhombic apertures.

The three most diverse Rhabdomesina families, the Rhabdomesidae, Rhomboporidae and the Hyphasmoporidae all show congruence in their mean BSI values that for their constituent genera cluster around the mid-30s (Table 1, Figure 2A). This moderately high BSI value is mainly related to increased exozonal width when compared to the Arthrostylids.

Genera within the Order Trepostomata exhibit a wide variety of zoarial forms from robust ramose erect branching forms, to hemispherical forms, and thin encrusting unilaminar or multilaminar sheets. The bryozoan skeleton may be subdivided into zooidal and extrazooidal skeleton with the latter contained within zooidal boundaries and the latter outside (Boardman & Buttler 2005). Trepostome zooids may be polymorphic with feeding autozooids most frequent, and in some families, exilazoecia and mesozoecia may be common. Within these, internal partitions such as diaphragms, hemiphragms or cystiphragms may be present that subdivide the zooidal chamber or slightly reduce its living chamber volume. Extrazooidal features include wall structures of several constructions and skeletal styles. It is difficult to distinguish the boundary between zoecial and extrazoecial skeleton (Boardman & Buttler 2005,

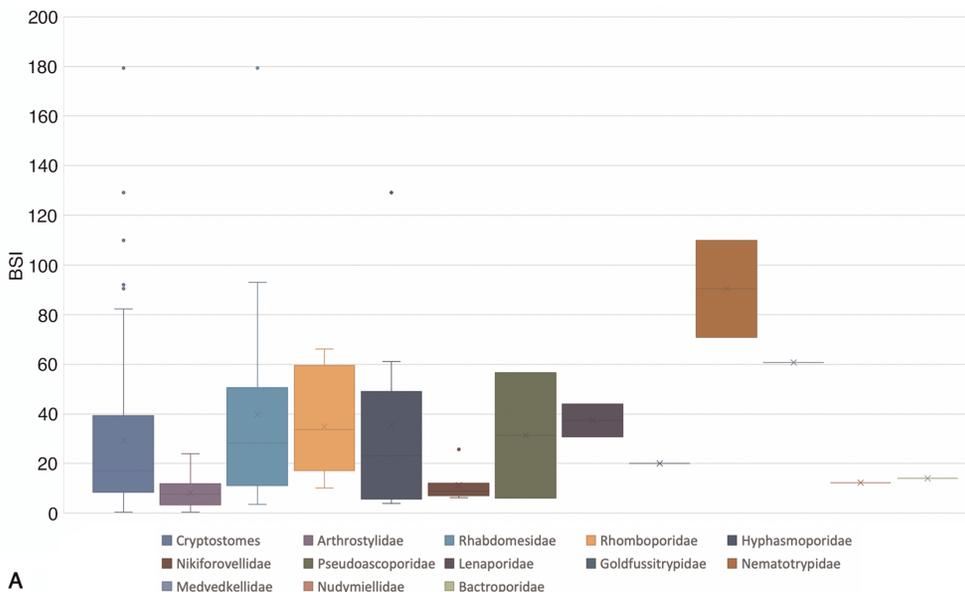


Figure 2. BSI in the orders (A) Cryptostomata and (B) Trepostomata and selected families and genera. In these box and whisker plots the Minimum and Maximum values are given by the position of the lower and upper whiskers respectively, the Quartile 1 and 3 values by the lower and upper edges of the box, while the Median is plotted with the dashed line and the Mean by an X.

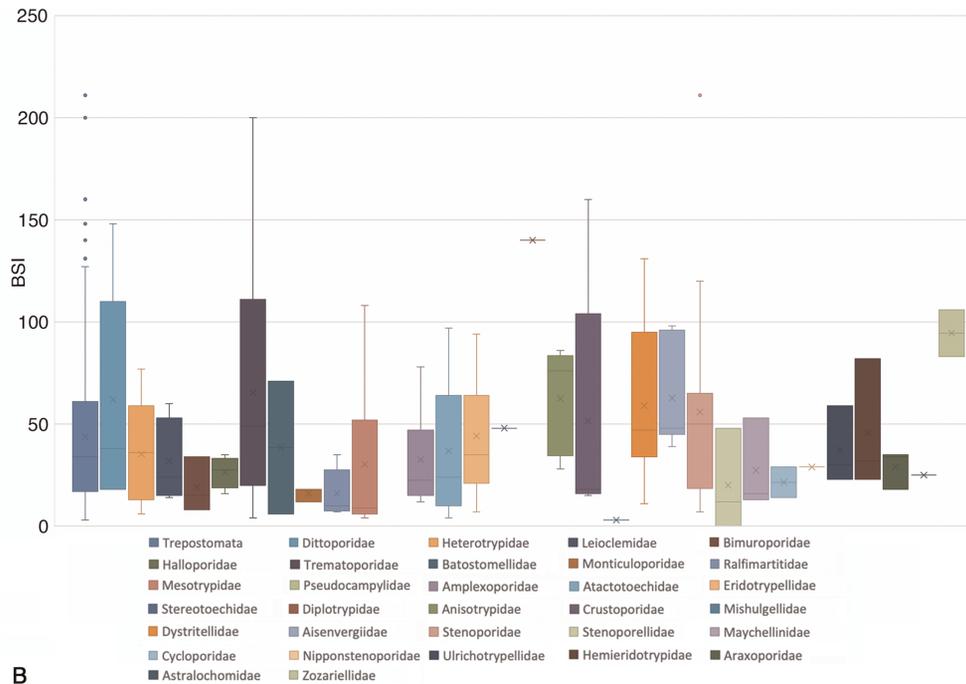


Figure 2. (Continued)

p. 1095) and some of the exozone skeleton is probably extrazoooidal. Autozoocidia in ramose colonies are budded from a well or ill-defined axial region, have long chambers in the endozone, and vestibules orientated at a high angle to the zoaria surface in the exozone. Diaphragms and other structural elements in chambers are frequently developed as are polymorphs such as mesozooecia and exilazooecia that are situated within the exozonal tissue. The exozone is usually composed of thickened skeletal walls in which acanthostyles may be developed. In some taxa, such as *Diplotrypa*, the exozone walls remain thin.

In the Order Trepostomata, BSI ranges from 3 in *Mishulgella* Gorjunova, 2001, an encrusting form from the Pennsylvanian of Russia (Figure 4A) to 211 in the robust erect Permian genus *Stenodiscus* Crockford, 1945. Highest mean BSI values occur in the trepostome families Crustoporidae (51.6), Stenoporidae (57.3), Dyscritellidae (59), Dittoporidae (62), Anisotrypidae (62.4), Aisenvergiidae (62.7) and Trematoporidae (65.4)

(Figure 2B). The lowest are in the Monticuloporidae (16), Ralfimartitidae (16), and Bimuroporidae (19). However, high mean values in a family don't necessarily demonstrate that all constituent genera have high BSI values. In the Stenoporidae the range is 204 from a low of 7 in *Pycnopora* Girty, 1911 to 211 in *Stenodiscus*, resulting from the fact that the former creates thin encrusting adnate sheets and the latter is ramose with a wide

exozone of thick moniliform walls. In the Trematoporidae the range in BSI is 196 (from 4 in *Acanthotrypina* Vinassa de Regny, 1921 to 200 in *Minussina* Morozova, 1960 in which the exozone thickness is pronounced (Tolokonnikova 2009)). Conversely in some families such as the Monticuliporidae the BSI range is low (12 in *Acantholaminatus* Marintsch, 1998 to 18 in both *Monticulopora* d'Orbigny, 1849 and *Gortanipora* Vinassa de Regny, 1921) reflecting the consistent narrow exozone shared by the genera in the family. Of the five genera in the Crustoporidae for which BSI was calculated, three returned low values and all have an encrusting habit as suggested they should have by the family appellation and placement, but two yielded high values including *Hunanopora* Yang, 1950 (48) and *Tabuliporella* Nikiforova, 1933 (160) with their ramose, erect colonies. Perhaps BSI might be beneficial in distinguishing potential systematic outliers in some taxa whether they be at family or below.

#### 4.2 Morphology, extrazoooidal characters and BSI

Which of the three defining morphological characters most influence BSI? We use Spearman's rank order correlation  $r_s$ , as the data do not have a normal distribution, and  $p$  values between the BSI characters and the BSI value to answer this question. For  $r_s$  values closer to  $-1$  or  $1$ , they indicate a negative or positive correlation, and closer to  $0$  indicate no correlation.

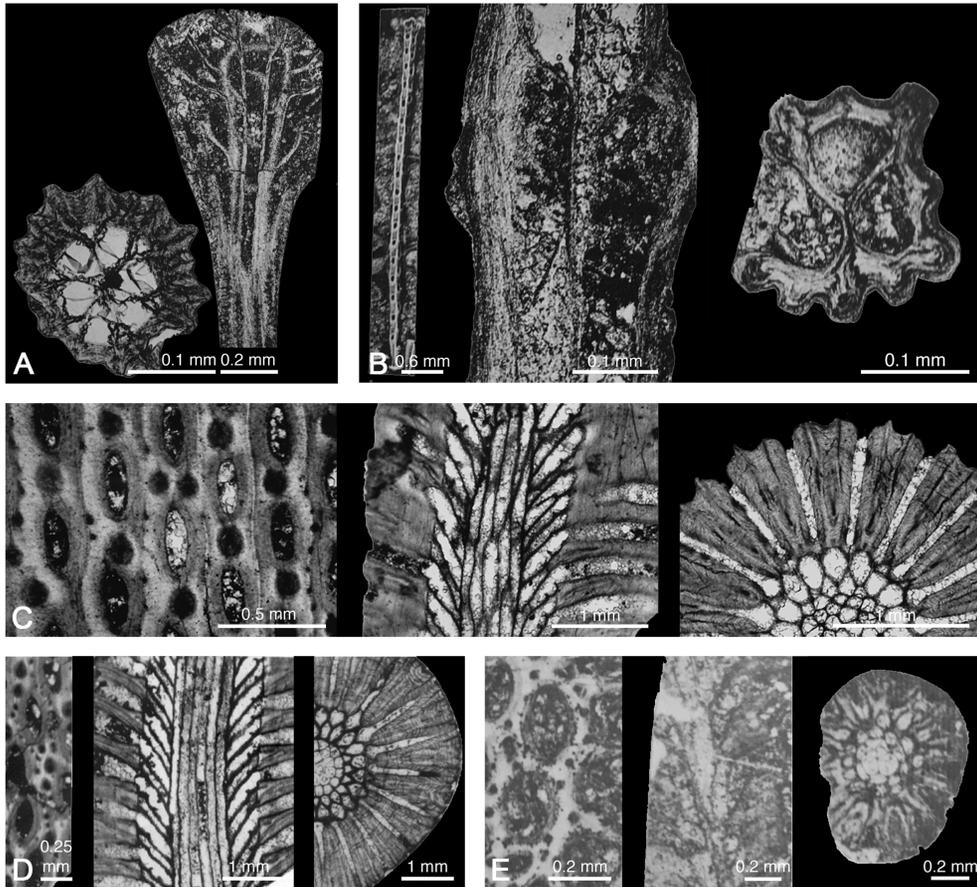


Figure 3. Examples of genera in the cryptostomata Family Arthrostylidae (A-B) and Suborder Rhabdomesina (C-E) with either high or low BSI values. (A) *Sceptropora facula* Ulrich, 1888 (BSI: 24); (B) *Arthrostylus tenuis* (James 1878) (BSI: 0.5); (C) *Muromipora smirnovi* Gorjunova, 2011 (BSI: 179.4); (D) *Ascopora florata* Schulga-Nesterenko, 1955 (BSI: 90.5); (E) *Promediapora transcaucasica* Gorjunova, 1992 (BSI: 3.6). [A-B from Utgaard 1983, C from Gorjunova 2011a, D from Gorjunova 2001, E from Gorjunova 1996].

Values for  $p$  above 0.05 indicate no significant correlation, but  $p$  values below 0.05 indicate more influence one of the three variables (i.e., exozone width (EW), autozoocial aperture diameter (MZD), and zoocial wall thickness (ZWT) has on predicting BSI. In both the trepostomes and the cryptostomes,  $r_s$  values are closer to 0 and  $p$  values are  $> 0.05$  for MZD – there is no significant control on BSI by MZD. For EW and ZWT,  $r_s$  values are higher and  $p$  values all well below 0.05 – EW and ZWT have significant influence on BSI (Figure 5A-F), but the latter may show variation depending on the depth of section.

#### 4.3 Insights from specific taxa or families

##### 4.3.1 Family Nematotrypidae

If taken as a member of the Arthrostylidae, *Cyclophaenopora* Spjeldnaes, 1984 is an outlier with BSI values of 110.0 which is five times higher than the next lower genus in the family, *Sceptropora*

Ulrich, 1888. This suggests that *Cyclophaenopora* may not be correctly assigned to this family. *Nematotrypa* Bassler, 1911 has a BSI of 70.9 which is closer to *Cyclophaenopora* to which it may be closely allied; this supports the placement of these two taxa in the Family Nematotrypidae (Nekhorosheva 2007). The taxonomic relationship of these two taxa is currently under investigation in a separate study by Ernst, Tolokonnikova and Wyse Jackson. In contrast, *Moyerella*, which Blake (1983c) included as an arthrostylid and Gorjunova (1985) and Ernst & Carrera (2008) as a nematotrypid, has a lower BSI of 8.5. If one takes a low BSI value as a familial defining character, then the genus would be best placed in the Arthrostylidae as per Blake (1983c) but a detailed morphological assessment of a species of *Moyerella* from the Ordovician of Argentina (Ernst & Carrera 2008 suggests that it belongs to the Family Nematotrypidae as Gorjunova (1985) originally wrote.

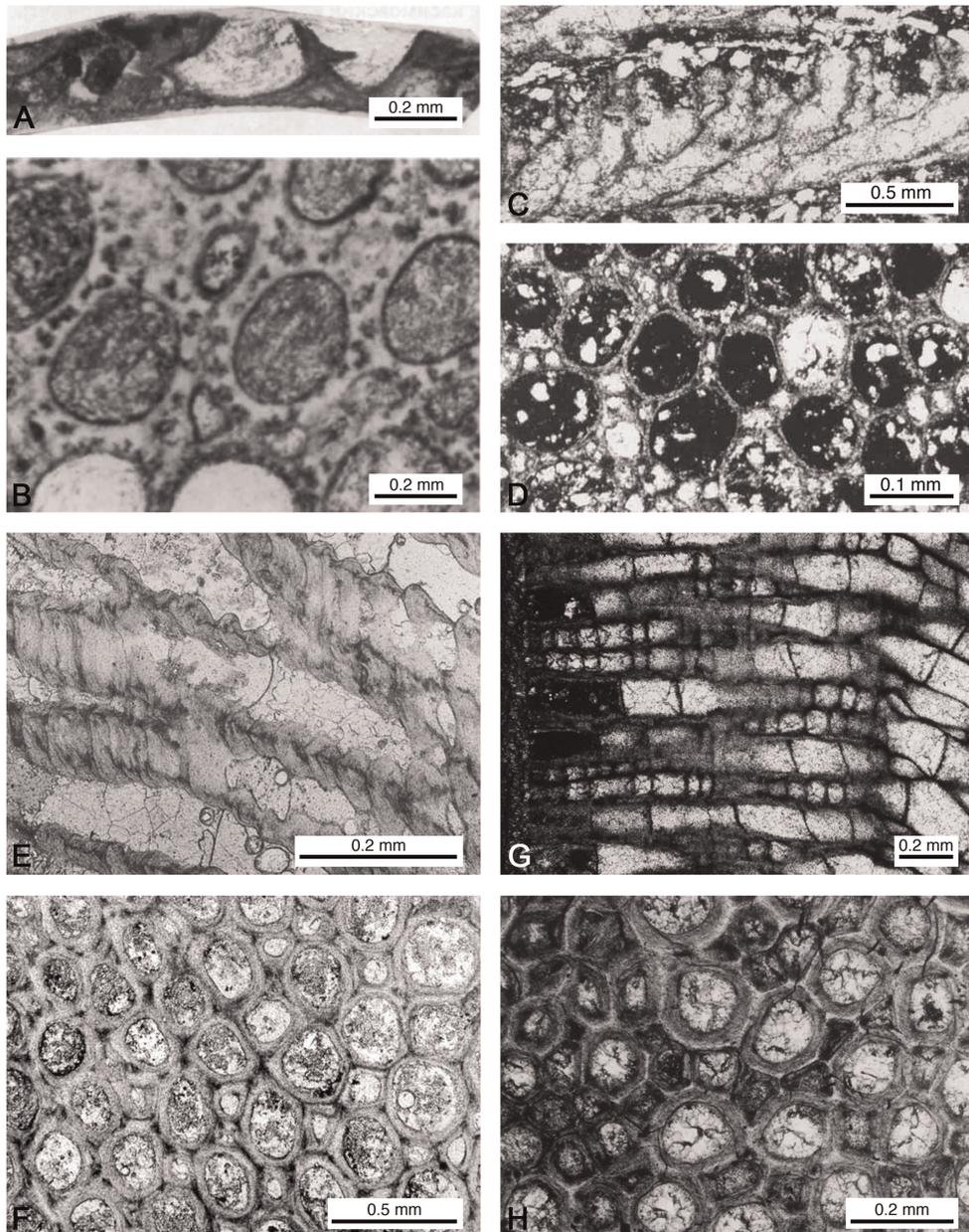


Figure 4. Examples of genera in the trepostomata with either low or high BSI values. (A-B) *Mishulgella stellata* Gorjunova, 2001 (BSI: 3); (C-D) *Pycnopora regularis* Girty, 1911 (BSI: 7); (E-F) *Stenodiscus moniliformis* Crockford, 1945 (BSI: 211); (G-H) *Minussina maculosa* Morozova, 1960 (BSI: 200) [A-B from Gorjunova 2001, C-H from Boardman and Buttler unpublished].

#### 4.3.2 Family Coelotubuliporidae

In the genera assigned to the Family Coelotubuliporidae by Gorjunova (2011b), BSI values range from 1.3 in *Coelotubulipora irregularis* (Nekohorshev 1956) from the Devonian of Siberia and *C. interminuta* Yang *et al.* 1988 from the Mississippian of Hunan, China to 13.1 in *C. euspimusa clautubulosa* Yang *et al.*, 1988 from the

same horizon and location in China. The mean BSI for the genus *Coelotubulipora* is 5.1 which is in contrast with the other constituent genus *Dunaevella* in which BSI is higher in both of its species: 24.8 and 87 (Table 2).

Species in *Coelotubulipora* are characterized by possessing a central axial tube that resembles closely that which is the diagnostic generic feature of

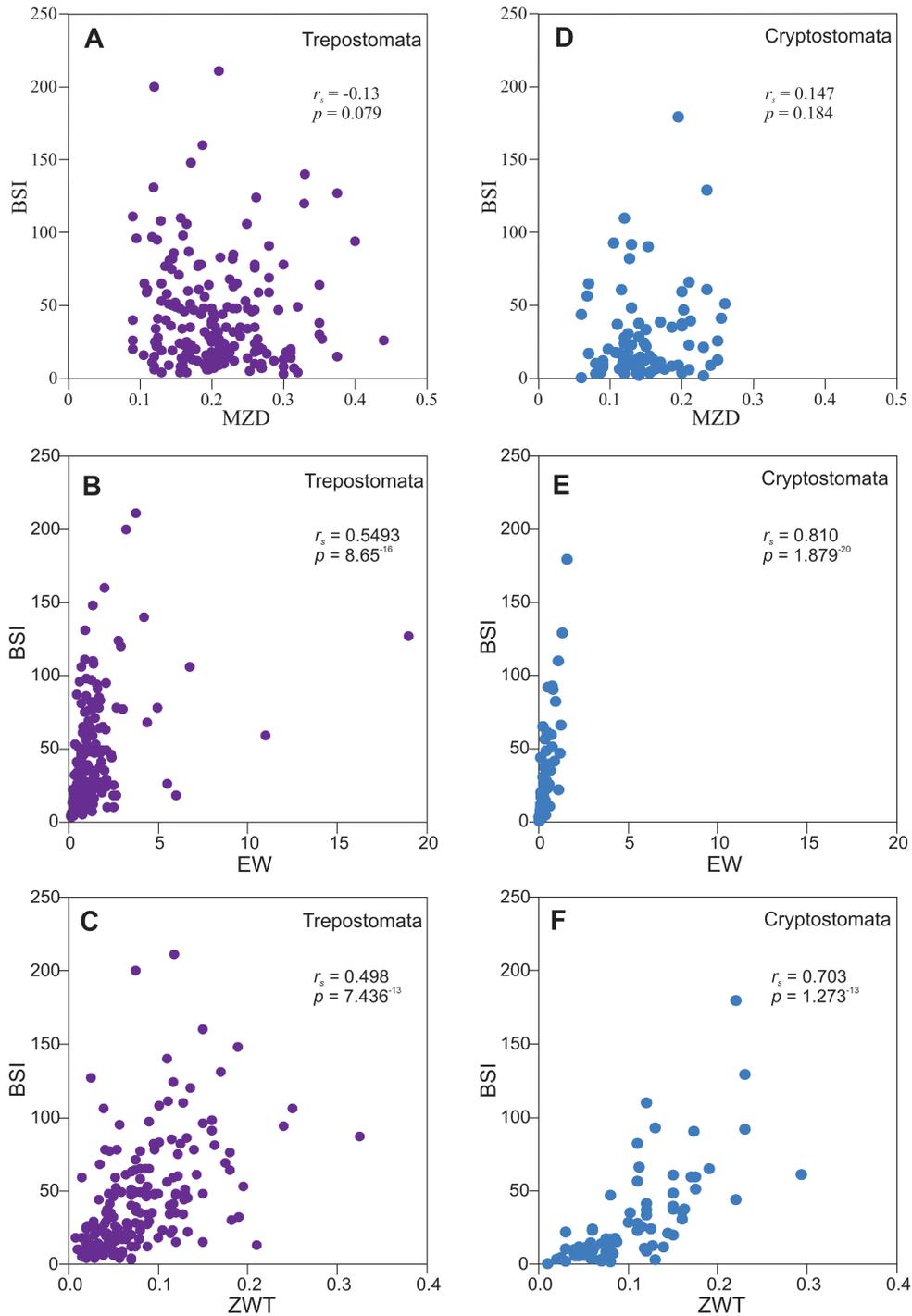


Figure 5. (A-C) BSI vs. morphological characters in trepostome genera; (D-F) BSI v. morphological characters in cryptostome genera. Measurements of morphological characters in mm.

the cryptostome genus *Rhabdomeson* Young & Young, 1874 (Wyse Jackson & Bancroft 1985) (Figure 6). It is therefore not surprising that Morozova *et al.* (2006) transferred the genus from

the trepostomes, where it was initially placed by Yang *et al.* (1988), to the cryptostomes. However, Gorjunova (2011b) argued that *C. rana* described by Morozova *et al.* (2006) belongs to

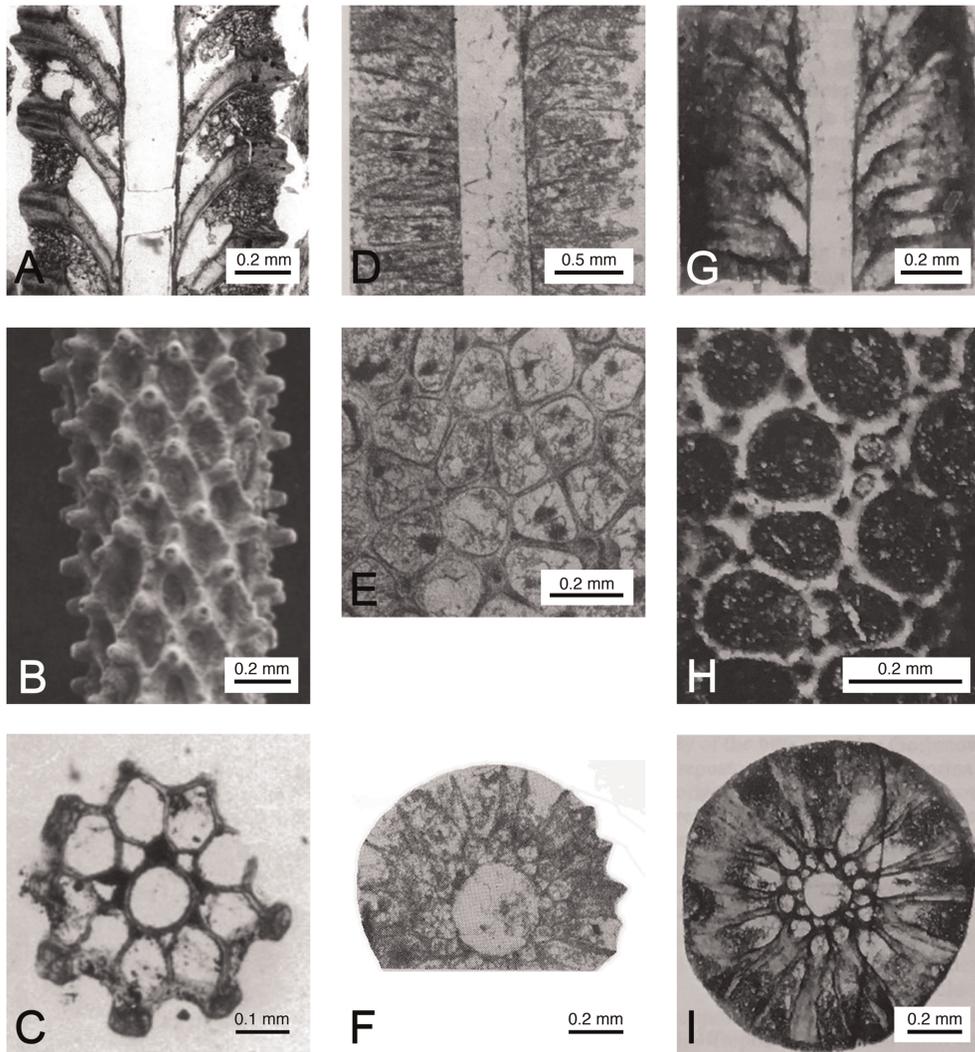


Figure 6. *Rhabdomeson* and taxa in the Family Coelotubuliporidae showing gross similarities in central axis but differences in autozoecial apertural arrangement and acanthostyle distribution; (A-C) *Rhabdomeson progradile* Wyse Jackson & Bancroft, 1985 (BSI: 3.9); (D-F) *Coelotubulipora eupinusa* Yang, Hu & Xia, 1988 (BSI: 10.6); (G-I) *Dunaevelia shishovae* (Schulga-Nesterenko 1955) (BSI: 87) [A-C from Wyse Jackson & Bancroft 1985, D-F from Yang, Hu & Xia 1988, G-I from Gorjunova 2011b].

*Rhabdomeson* and not *Coelotubulipora*, and that species placement in the latter is based not only on the central axial tube but other additional morphological characteristics. In *Coelotubulipora*, the autozoecial apertural arrangement is not regular in longitudinal rows, the budding pattern from the axis is more irregular as is the distribution of stylites on interapertural walls, and exozonal zoecial walls are very thin, unlike those developed in *Rhabdomeson*. Although the low mean BSI is similar to *Rhabdomeson* and suggests that *Coelotubulipora* is closely allied to it using this solitary measure, the other morphological characteristics counter this argument and Gorjunova's

(2011b) placement of *Coelotubulipora* in the Trepostomata is supported by BSI.

#### 4.3.3 *Tebitopora*

Identification of the complexities of skeletal material and the budding patterns of autozoecia, together with the development or absence of polymorphs allow for assignment of taxa to steno-laemate families and orders. The genus *Tebitopora* described from the Triassic of Tibet by Hu (1984) was originally considered to contain two species, *T. orientalis*, the type species, and *T. depressa* but is now known to be monospecific (Ma *et al.* 2020). BSI may well be a crude measure for supra-generic

taxonomic determinations, but in the case of *Tebitopora* which has been placed in two orders since its initial description, its BSI value is 22 (Table 2) which is in keeping with Late Paleozoic cryptostomes and is lower than all but one Triassic genera that have been assigned to the Trepostomata: *Arcticopora* (131), *Buria* (64), *Dyscritellopsis* (47), *Metastenodiscus* (78), *Phragmotrypa* (36), *Vysokella* (83) and *Zozariella* (106); the only exception being *Reptonoditrypa* (13).

## 5 CONCLUSIONS

In the orders Cryptostomata and Trepostomata, BSI is largely controlled by exozone width and interapertural wall thickness while autozooecial apertural diameter is not as significant.

The placement of a number of Upper Paleozoic stenolaemate genera remains problematic on account of the presence of structural and zooecial morphologies considered by researchers to be characteristic of both orders. In rhabdomesonid cryptostomes such as *Muromipora* (BSI: 179.4) exozone thickness increases to constitute over two-thirds of branch diameter so that taxa are more robust like their trepostome counterparts, or as in *Ogbinopora* Shishova, 1965 (BSI: 129.2) exozone width is significantly thicker than in most cryptostomes thus contributing a high degree of skeletal material.

In the Suborder Rhabdomesina, BSI mean values increase from the Silurian to the Pennsylvanian but decreases in later geological periods. Over the same geological timespan, BSI mean values in the Order Trepostomata are more consistent. The BSI value of *Tebitopora* is low and differs from that in unequivocal Triassic trepostomes and so BSI supports its placement in the Order Cryptostomata.

*Moyerella* which has a low BSI akin to the arthrostylids may be more correctly placed in the Family Nematotrypidae in the Trepostomata on structural and morphological grounds as demonstrated by Ernst and Carrera (2008). The same conclusion and reasoning should be applied in retaining the Family Coelotubuliporidae in the Trepostomata rather than in the Suborder Rhabdomesina even though BSI values of *Coelotubulipora* species are low like other rhabdomesinids.

BSI values calculated for genera within families may not be consistently similar. This study demonstrates that utilization of BSI as a taxonomic distinguishing characteristic is not reliable, but simply an indicator to be utilized alongside all available morphological data on which a greater emphasis should be placed. It should be viewed as a similar derived character such as Boardman's axial ratio (Boardman 1960) which is commonly calculated in systematic descriptions. BSI should be

computed for new taxa or those undergoing revision, so that generic BSI values may be considered against that from other genera in the same family (as might be done for members in the trepostome Family Crustoporidae), and for new or earlier described species so that comparisons can be made. Similarly, any suprageneric revisions may find value in computing BSI values of candidate genera for placement in families. Outliers in values would merit further investigation and carefully considered subsequent taxonomic placement of taxa.

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## REFERENCES

- Astrova, G.G. 1978. Historical Development, Systematics and Phylogeny of Bryozoa. Order Trepostomata. *Trudy Paleontologicheskogo Instituta Akademiyi Nauk SSSR* 169: 1–240 [In Russian].
- Bassler, R.S. 1911. The Early Paleozoic Bryozoa of the Baltic Provinces. *United States National Museum Bulletin* 77: 1–382.
- Blake, D.B. 1975. The Order Cryptostomata Resurrected. In S. Pouyet (ed.), *Bryozoa 1974. Documents de Laboratoires de Géologie Faculté de sciences de Lyon, hors-serie 3* (1): 211–223.
- Blake, D.B. 1983a. The Order Cryptostomata. In R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part G, Revised, Bryozoa*: 440–452. Boulder & Lawrence: Geological Society of America & University of Kansas Press.
- Blake, D.B. 1983b. Introduction to the Suborder Rhabdomesina. In R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part G, Revised, Bryozoa*: 530–549. Boulder & Lawrence: Geological Society of America & University of Kansas Press.
- Blake, D.B. 1983c. Systematic Descriptions of the Suborder Rhabdomesina. In R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part G, Revised, Bryozoa*: 550–592. Boulder & Lawrence: Geological Society of America & University of Kansas Press.
- Boardman, R.S. 1960. Trepostomatous Bryozoa of the Hamilton Group of New York State. *United States Geological Survey Professional Paper* 340: 1–87.
- Boardman, R.S. & Buttler, C.J. 2005. Zooids and Extrazooecial Skeleton in the Order Trepostomata (Bryozoa). *Journal of Paleontology* 79: 1088–1104.
- Bock, P. *Bryozoa Home Page; Family Arthrostylidae*. <http://bryozoa.net/cryptostomida/arthrostylidae/index.html> (accessed 3 July 2022)

- Cohen, K.M., Harper, D.A.T., Gibbard, P.L. & Fan, J.-X. 2020. *The ICS International Chronostratigraphic Chart, version 2020/03*. International Commission on Stratigraphy. <https://stratigraphy.org/ICSChart/ChronostratChart2020-03.pdf>
- Crockford, J.M. 1945. Stenoporids from the Permian of New South Wales and Tasmania. *Proceedings of the Linnean Society of New South Wales* 70: 9–24.
- d'Orbigny, A. 1849. *Prodrome de Paléontologie Stratigraphique Universelle des Animaux Mollusques et Rayonnés faisant suite au Cours élémentaire de Paléontologie et géologie Stratigraphiques* Vol. 1, 1–394. Paris: Masson.
- Ernst, A. & Carrera, M. 2008. Cryptostomid Bryozoans from the Sassito Formation, Upper Ordovician Cool-water Carbonates of the Argentinean Precordillera. *Palaeontology* 51: 1117–1127.
- Girty, G.H. 1911. New Genera and Species of Carboniferous Fossils from the Fayetteville Shale of Arkansas. *Annals of the New York Academy of Science* 20: 189–238.
- Gorjunova, R.V. 1985. Morphology, System and Phylogeny of Bryozoa (Order Rhabdomesida). *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 208: 1–152 [In Russian].
- Gorjunova, R.V. 1992. Morphology and System of the Paleozoic bryozoans. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 251: 1–168 [In Russian].
- Gorjunova, R.V. 1996. Phylogeny of the Paleozoic bryozoans. *Trudy Paleontologicheskogo Instituta* 267: 1–165 [In Russian].
- Gorjunova, R.V. 2001. Bryozoa. In A.S. Alekseev & S. M. Shik (eds), *Middle Carboniferous of Moscow Syncline (southern part). Volume 2. Biostratigraphy*: 80–91. Moscow: Scientific World [In Russian].
- Gorjunova, R.V. 2011a. Carboniferous Bryozoans of the Order Rhabdomesida of the East European Platform. *Paleontological Journal* 45: 1–106.
- Gorjunova, R.V. 2011b. Family Coelotubuliporidae Fam. Nov. and Morphological Parallelisms in the Evolution of Bryozoans. *Paleontological Journal* 45: 510–524.
- Hu, Z. 1984. Triassic Bryozoa from Xizan (Tibet) with Reference to Their Biogeographical Provincialism in the World. *Acta Palaeontologica Sinica* 23: 568–577.
- James, U.P. 1878. Descriptions of Newly Discovered Species of Fossils from the Lower Silurian Formation, Cincinnati group. *The Palaeontologist* 1, 1–8.
- Karklins, O.L. 1983a. Introduction to the Suborder Ptilodictyina. In R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part G, Revised, Bryozoa*: 453–488. Boulder & Lawrence: Geological Society of America & University of Kansas Press.
- Karklins, O.L. 1983b. Systematic Descriptions of the Suborder Ptilodictyina. In R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part G, Revised, Bryozoa*: 489–529. Boulder & Lawrence: Geological Society of America & University of Kansas Press.
- Key, M.M., Jr., Wyse Jackson, P.N. & Reid, C.M. 2022. Trepostome Bryozoans Buck the Trend and Ignore Calcite-aragonite Seas. *Palaeobiodiversity and Palaeoenvironments* 102: 253–263.
- Ma, J., Buttler, C.J. & Taylor, P.D. 2020. The Last Known Cryptostome Bryozoan? *Tebitopora* from the Tibetan Triassic. In P.N. Wyse Jackson & K. Zagorsek (eds), *Bryozoan Studies 2019*: 91–98. Prague: Czech Geological Survey.
- Marintsch, E.J. 1998. Systematic Paleontology, Biostratigraphy and Paleoecology of the Middle Ordovician Bryozoan (Trepostomata) from the Hermitage Formation of East-central Tennessee. *Bulletins of American Paleontology* 112: 1–121.
- Morozova, I.P. 1960. Devonian Bryozoa of the Minusinsk and Kuznetsk Basins. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 86, 1–207 [In Russian].
- Morozova, I.P., Weiss, O.B. & Racki, G. 2006. New Devonian and Carboniferous Bryozoans of the Holy Cross Mountains (Central Poland). *Paleontological Journal* 40: 529–540.
- Nekhoroshev, V.P. 1956. Lower Carboniferous Bryozoa of the Altai and Siberia. *Trudy Vsesoyuznyy Nauchno-Issledovatel'skiy Geologicheskii Institut (VSEGEI)*, n. s., 13: 1–419 [In Russian].
- Nekhorosheva, L.V. 2007. Results of Paratype Research on the Type Species *Cyclophaenopora* Spjeldnaes, 1984 (Bryozoa, Family Nematotrypidae). *Nature and Economy of Kuzbass. Regional proceedings*. Kuzbass Pedagogical Academy, Novokuznetsk: KuzGPA Publishing House, 11: 35–37 [In Russian].
- Nicholson, H.A. 1879. *On the Structure and Affinities of the "Tabulate Corals" of the Paleozoic Period, with Critical Descriptions of Illustrative Species*. Edinburgh: William Blackwood and Sons.
- Nikiforova, A.I. 1933. The Carboniferous Deposits of Central Asia: Contributions to the Knowledge of the Lower Carboniferous Bryozoa of Turkestan. *Trudy Vsesoyuznogo Geologorazvedochnogo Ob'edineniya* 207, 1–76.
- Ozhgibesov, V.P. 1983. *Permoheloclema* – a New Bryozoan Genus of the Order Rhabdomesida. *Paleontologicheskii Zhurnal* 1983 (4): 96–98.
- Powers, C.M. & Pachut, J.F. 2008. Diversity and Distribution of Triassic Bryozoans in the Aftermath of the End-Permian Mass Extinction. *Journal of Paleontology* 82: 362–371.
- Reid, C.M. 2021. A redescription of *Stenopora* and the Type Species *Stenopora tasmaniensis* Lonsdale, 1844 (Trepostomata, Bryozoa). *Journal of Paleontology* 95: 1147–1157.
- Reid, C.M., Wyse Jackson, P.N. & Key, M.M., Jr. 2022. Latitudinal Influences on Bryozoan Calcification Through the Paleozoic. *Paleobiology*. doi: 10.1017/pab.2022.31
- Schäfer, P. & Grant-Mackie, J.A. 1998. Revised Systematics and Palaeobiogeography of Some Late Triassic Colonial Invertebrates from the Pacific Region. *Alcheringa* 22: 87–122.
- Schulga-Nesterenko, M.I. 1955. Carboniferous Bryozoa from the Russian Platform. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 58: 1–207 [In Russian].
- Shishova, N.A. 1965. The Systematic Position and Size of the Family Hyphasporidae. *Paleontologicheskii Zhurnal* 1965 (2): 55–62 [In Russian].
- Spjeldnaes, N. 1984. Upper Ordovician Bryozoans from Ojl Myr, Gotland, Sweden. *Bulletin of the Geological Institutions of the University of Uppsala, n.s.*, 10: 1–66.
- Taylor, P.D. 1993. Bryozoa. In M.J. Benton (ed.), *The Fossil Record 2*: 477–489. London: Chapman & Hall.
- Tolokonnikova, Z.A. 2009. Biogeography and Evolution of Bryozoans of the Genus *Minussina* Morozova, 1961. *Paleontological Journal* 43: 391–400.

- Trizna, V.B. 1958. Early Carboniferous Bryozoans of the Kuznetz Depression. *Trudy Vsesoyuznyi Nauchno-Issledovatel'skii Geologo-Razvedochnyii Neftanoi* 122: 1–436 [In Russian].
- Ulrich, E.O. 1882. American Palaeozoic Bryozoa. *Journal of the Cincinnati Society of Natural History* 5: 121–175, 233–257.
- Ulrich, E.O. 1888. On *Sceptropora*, a New Genus of Bryozoa, with Remarks on *Helopora*, Hall, and Other Genera of That Type. *American Geologist* 1, 228–234.
- Utgaard, J. 1983. Systematic Descriptions for the Order Cystoporata. In R.A. Robison (ed.), *Treatise on Invertebrate Paleontology, Part G, Revised, Bryozoa*: 358–439. Boulder & Lawrence: Geological Society of America & University of Kansas Press.
- Vinassa de Regny, P.E. 1921. Sulla Classificazione Dei Trepostomata. Atti della Società italiana di scienze naturali, e del Museo civico di storia naturale. *Milano* 59: 212–231.
- Vine, G.R. 1884. Fourth Report of the Committee, Consisting of Dr. H. C. Sorby and Mr. G. R. Vine, Appointed for the Purpose of Reporting on Fossil Bryozoa. In *Report of the British Association for the Advancement of Science (Southport, 1883)*: 161–209. London: John Murray.
- Wyse Jackson, P.N. & Bancroft, A.J. 1985. Generic Revision of the Cryptostome Bryozoan *Rhabdomeson* Young and Young, 1874, with Descriptions of Two Species from the Lower Carboniferous of the British Isles. *Journal of Paleontology* 69: 28–45.
- Wyse Jackson, P.N., Key, M.M., Jr., & Reid, C.M. 2020. Bryozoan Skeletal Index (BSI): A Measure of the Degrees of Calcification in Stenolaemate Bryozoans. In P.N. Wyse Jackson & K. Zagorsek (eds), *Bryozoan Studies 2019*: 193–206. Prague: Czech Geological Survey.
- Yang, J. 1950. Some Bryozoans from Upper Devonian and Lower Carboniferous of Hunan. *Paleontological Society China* 6: 1–16 [In Chinese].
- Yang, J., Hu, Z. & Xia, F. 1988. Bryozoans from Late Devonian and Early Carboniferous of Central Hunan. *Palaeontologia Sinica* 174, Series B (23): 1–197.
- Young, J. & Young, J. 1874. On a New Genus of Carboniferous Polyzoa. *Annals and Magazine of Natural History, series 4*, 13: 335–339.