Paleobiology, 46(2), 2020, pp. 218–236
DOI: 10.1017/pab.2020.13

PALEOBIOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

Article

In search of predictive models for stenolaemate morphometry across the skeletal–polypide divide

Yuta Tamberg and Abigail M. Smith

Abstract.—Marine bryozoans have been members of benthic skeletal faunas since the Ordovician. These small suspension feeders collect particles in the range of 10 to 100 µm. Specific details of their feeding depend on the morphology of the feeding apparatus, which may be reflected in skeletal characters. While several studies have described the link between the skeletal and soft-body traits of gymnolaemate bryozoans, stenolaemates have received less attention. To fill this gap, we conducted a detailed analysis of morphometry within and across species and attempted to develop robust predictive models that can be used to infer the soft-body morphology from skeletal data. This, in turn, will help with extracting data on ecology of Paleozoic communities of suspension feeders from the extensive bryozoan fossil record. Characters of polypide morphology among New Zealand cyclostomates (single Recent order in Stenolaemata) displayed staggering variability and almost without exception were not connected to skeletal characters at the species level. When this variability is reduced to its central tendency, interspecific trends are more apparent. The relationship is positive, linear, and moderately strong, but the resulting models have wide predictive intervals (plus/minus hundreds of micrometers). A precise estimate of the characters of the feeding apparatus of modern, and especially fossil, stenolaemates may be difficult to attain, at least on the basis of the skeletal traits used here.

Yuta Tamberg and Abigail M. Smith. Department of Marine Science, University of Otago, P.O. Box 56, Dunedin, New Zealand. E-mail: yutamberg@gmail.com, abby.smith@otago.ac.nz

Accepted: 22 February 2020
Data available from the Pangaea Digital Repository: https://doi.pangaea.de/10.1594/PANGAEA.904628

Introduction

Bryozoans are small benthic suspension feeders that play important roles in marine communities, especially in the Southern Hemisphere. Among the three classes of bryozoans, Phylactolaemata are found in fresh water, Gymnolaemata are predominantly marine, and Stenolaemata are exclusively marine. Most stenolaemate taxa are ancient and only known from the fossil record, with Cyclostomatida the sole surviving order.

Bryozoans are colonial animals, and each colony module, or zooid, is traditionally divided into a cystid (the zooid wall) and polypide (which can be retracted into the cystid or partly everted from it). The cystid includes the living portion of the zooid body wall and a nonliving, often calcified, portion (including cuticle) that provides structural support. The polypide comprises the gut, lophophore with tentacles, introvert, muscles, and ganglion (e.g., Borg 1926; Ryland 1970) (Fig. 1).

Together, introvert and lophophore make up the specialized feeding apparatus of bryozoans. The introvert is the part of the polypide that serves as a flexible stalk supporting the lophophore when everted and as a tentacle sheath when retracted. The lophophore is a widened platform around the mouth that bears a fringe of ciliated tentacles and contains a coelomic cavity. In Phylactolaemata the lophophore is U-shaped, while Gymnolaemata and Stenolaemata have circular lophophores.

The tentacles are the main food-gathering elements of the lophophore; they bear cilia that generate currents and take part in capturing or rejecting particles. Each tentacle typically bears two or three types of ciliary bands: frontal, latero-frontal, and lateral (Mukai et al. 1997). The latter are the longest and play the principal role in feeding, because their strokes generate water currents (Borg 1926).

Naturally, cystid and polypide morphology are interconnected (see, e.g., summary by

0094-8373/20

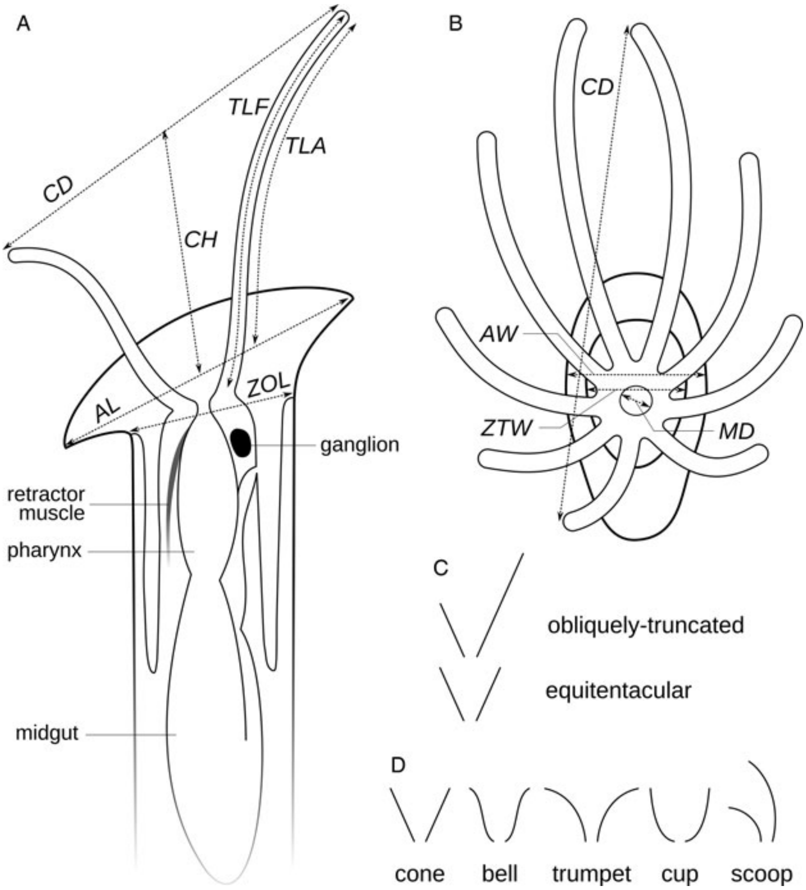

FIGURE 1. Schematic drawings of the proximal parts of the bryozoan polypide, showing characters recorded in this study. A, A scheme of a sagittal section through the zooid with everted polypide. B, Top view of the protruded polypide. C, Types of the tentacle crown symmetry. D, Types of the crown shape, resulting from different tentacle curvatures.
AL, aperture length; AW, aperture width; CD, diameter of the tentacle crown; CH, height of the tentacle crown above the aperture; MD, mouth diameter; TLA, length of the tentacle visible above the aperture; TLF, full tentacle length; ZOL, length of the zooid tube opening at the orifice level; ZTW, zooid tube width at the orifice level.

McKinney 1990). Polypide size and shape are dictated by adaptation to feeding; the dimensions of the feeding apparatus are related to the dimensions of captured food (Winston 1977; Sanderson et al. 2000). Also, the characters of the tentacle crown—its diameter and the length and number of the tentacles—are directly related to the number of lateral cilia (Ryland 1970, 1976; Riisgård and Manríquez 1997), and thus to feeding current speeds (Best and Thorpe 1986), pumping (Riisgård and Manríquez 1997), and clearance rates (Strathmann 1973; Winston 1977).

In addition, the protrusion–retraction mechanism employed by bryozoans limits the height/depth of tentacle protrusion, thus determining some morphological relationships (Taylor 1981). During protrusion, phylactolaemates and gymnolaemates change the shape of the zooid walls (either directly or by using thin-walled sacs filled with or emptied of seawater). By contrast, Recent stenolaemates have inflexible zooid walls and rely on their own body cavity fluid instead of seawater to compensate for lophophore protrusion. Their trunk coelom is split into exosaccal and endosaccal cavities, and the former compensates for shape changes of the latter (Nielsen and Pedersen 1979).

Everted polypides of cyclostomates do not protrude from cystids farther than the lophophore base; the introvert is often not seen, and the mouth lies level with or below the aperture (in other classes, both the lophophore and introvert are revealed). Given these conditions, Taylor (1981) proposed that (1) clearance rate is lower in cyclostomates, because some of the cilia are hidden below the skeletal rim; and (2) cyclostomates have a narrow range of behaviors because introvert movements are nearly absent (the latter is partially supported by Shunatova and Ostrovsky 2001).

Some parameters of zooid morphology appear to be nearly fixed within species, for example, the length of the cilia (data in Tamberg and Shunatova 2017: Table 2); proportions and spacing of the tentacles, for example, distances between tentacle tips (Ryland 1975; Herrera and Jackson 1992); and mouth size (Herrera and Jackson 1992). Others may vary more widely, for example, the size of the tentacle crown and tentacle length, number, and shape (Ryland 1975, 1976; Tamberg and Shunatova 2017), and the overall shape of the crown (Winston 1978; McKinney 1990; Shunatova and Ostrovsky 2001).

Several studies indicate that such soft-body parameters are also positively correlated with skeletal traits (McKinney and Boardman 1985; McKinney and Jackson 1991), enabling theoretical reconstruction of the soft-body parts of fossil specimens. This in turn allows a range of paleoecological and paleofaunistic interpretations, from estimating the size range of available food particles to assessing the relationships between bryozoan orders through time. The existing formulas, however, cover very few zooid traits.

In Gymnolaemata the morphometry of the feeding apparatus is well understood, with many reported measures and established relationships (Winston 1977, 1978, 1981; McKinney 1990). By contrast, Stenolaemata have not received nearly as much attention from researchers (Smith et al. 2017). It is a relatively large class with a rich fossil history (thousands of species from six extinct orders, dating back to the Ordovician) and about 543 living species in 98 genera in the extant order Cyclostomatida (Ryland 1970; Bock and Gordon 2013). Yet accounts of morphology of their soft parts and interrelationships with skeletal dimensions are extremely uncommon. Scattered morphometric data are given in various studies (Borg 1926, 1944; Ryland 1967, 1975; Winston 1977, 1978, 1979; Schäfer 1985; McKinney 1991; Ryland and Hayward 1991; Nielsen and Riisgård 1998; Shunatova and Ostrovsky 2001; Ramalho et al. 2009). Rarely, however, do such reports combine cystid and polypide measurements. Equally rare is an indication of how many colonies were examined to reach the reported conclusions.

The aim of the present study is, therefore, to examine Recent cyclostomate polypide morphology and allometry, concentrating on the relationships between soft-part and skeletal morphology. We undertook this study on the southern New Zealand shelf (latitudes 45°S to 47°S), a place with abundant and diverse cyclostomates (Gordon et al. 2009). We hope this will help paleontologists better interpret fossil stenolaemates.

Materials and Methods

We collected living colonies of cyclostomate species from around New Zealand, covering different taxonomic groups and a wide range of sizes and colonial forms. The majority of bryozoans were collected by dredge as part of a bimonthly sampling program in 2018 from a water depth of ~90 m on the Otago shelf of New Zealand (45°47.89′S, 170°54.5′E; Batson and Probert 2000). Additional samples were taken in April 2018 from 58 m and 77 m around Stewart Island (46°54.87′S, 168°13.06′E and 47°07.70′S, 168°10.79′E, respectively).

Living bryozoan colonies were cultured in flow tanks in an isothermic room at ~13°C. Colonies were left to recover from dredging for at least 3 days, and kept alive for 1–4 weeks. Throughout this time, the colonies were constantly supplied with a mixture of natural particles and cultured algae (*Rhodomonas salina* and *Dunaliella tertiolecta*). Feeding animals with fully extended lophophores were imaged with a camera mounted on a dissecting microscope. From 9 to 54 photographs were taken of each specimen.

Measurements were made from the photographs using Inkscape 0.48.1 (Inkscape Project 2011). We recorded 10–12 parameters for each specimen, covering both skeletal and soft-body traits (Fig. 1). There were four skeletal characters: length and width of the aperture (AL and AW) and length and width of the zooid tube opening near the orifice (ZOL and ZTW). Among four tentacle crown parameters, two were quantitative: crown diameter (CD) and height visible above the aperture (CH); and two were qualitative: crown symmetry (Fig. 1C) and curvature (Fig. 1D). Finally, the three tentacle parameters were: tentacle number (TN), full tentacle length (TLF, sometimes simplified to tentacle length, TL, later in the article), and tentacle length visible above the aperture (TLP). For species with obliquely truncated tentacle crowns, we additionally recorded the length of the longest and shortest tentacles. We also measured mouth diameter (MD). The raw dataset is stored in full at PANGEA (PDI-21252). In this paper, the measured traits are reported with parametric descriptive statistics (mean ± SD, N) to ensure comparability with data from other authors. For the qualitative characteristics of the crown shape (symmetry and curvature), we give the dominant value and its frequency contrasted with the combined frequency of all other values.

The species we collected were divided into two groups. The first group contained abundant, easily identified, mostly large, and robustly calcified species (Table 1, Fig. 2B–D), examined in great detail and forming the main dataset of the study. In this group we recorded zooid traits in at least 10 colonies of each of the eight large species (a total of 83–209 zooids per species). An additional five species, which were smaller and less heavily calcified, formed the supportive dataset (Table 1, Fig. 2A); they were examined in lesser detail from fewer specimens (20–42 zooids per species). Assembled photographs of each colony yielded 5–25 measurements, but due to the varying angles of the photographs, not all characters were covered with equal detail.

Before proceeding, we checked whether these two datasets captured the natural variability of quantitative characters within each species equally well. To do this, we compared coefficients of variation of each character distribution using the Wilcoxon rank-sum test. As no differences were found ($p > 0.26$), we concluded that both datasets give a similarly detailed picture of zooid traits and treated them together in subsequent analyses.

To uncover relationships between skeletal and soft-body traits within our datasets, we used Pearson's correlations based on specimen measurement pairs, pooled across species. A correlation matrix of skeletal traits was made to find which traits could be used as independent predictors in subsequent regressions. Correlations between soft-body characteristics themselves were calculated to provide context for skeleton–polypide relationships. We proceeded to calculate univariate linear regressions between selected skeletal parameter and soft-body traits. Regressions were made for each species independently, as well as for all species together.

To establish relationships between zooid parameters in the wider context of all bryozoan classes, we created a hybrid dataset including measurements from published sources and our measurements from the full and supplementary datasets (means, medians, and SDs). Many cited sources were patchy in their coverage of the zooid parameters, which produced an inherently unbalanced dataset. Thus, to cover as many measurement pairs as possible, we performed five separate linear regression analyses with the zooid tube width and class as universal predictors and five soft-body traits (CD, CH, TL, TN, MD) as response variables.

Evaluating the resulting models, we learned that *Cinctipora elegans* exerted the strongest influence on regression parameters (Cook's distances between 1.8 and 5.5), invariably reducing the slope of the line. This is hardly surprising, given the trumpet-like shape of the zooids. Exclusion of this species from all regression analyses is justified from the mathematical point of view and also because it is very unusual among cyclostomates. While other tubuliporines, rectangulates, and cancellates in this study could be readily compared with known extinct species, *C. elegans* lacks an analogue in the Paleozoic fossil record.

To test the predictive abilities of the models, we measured photographs of 2–5 zooids from nine unidentified cyclostomate species from suborder Tubuliporina, collected in the same locations as the main material of this study. We made as many measurements as possible

TABLE 1. Cyclostomate bryozoan species used in this study, collected off Otago and Stewart Island, New Zealand.

Species	Family	Colonies photographed	Zooids measured	Colony growth type
Main dataset				
Cinctipora elegans Hutton, 1873	Cinctoporidae	13	140	Erect rigid, robust branching
Diaperoecia purpurascens (Hutton, 1877)	Diaperoeciidae	10	121	Erect rigid, robust branching
Disporella pristis (MacGillivray, 1884)	Lichenoporidae	10	199	Encrusting monticulate
Favosipora rosea Gordon & Taylor, 2001	Densiporidae	10	177	Encrusting monticulate
Hornera foliacea MacGillivray, 1869	Horneridae	10	208	Erect rigid, robust branching
Hornera robusta MacGillivray, 1883.	Horneridae	10	209	Erect rigid, reticulate
Platonea sp.	Tubuliporidae	10	83	Encrusting unilaminar
Telopora lobata (Tenison-Woods, 1880)	Hastingsiidae	10	104	Erect rigid, radiate
Supporting dataset				
Diaperoecia sp.	Diaperoeciidae	3	20	Erect rigid, robust branching
Disporella sp.	Lichenoporidae	7	42	Encrusting monticulate
Doliocoitis cyanea Gordon & Taylor, 2001	Lichenoporidae	3	41	Encrusting monticulate
Idmidronea sp.	Tubuliporidae	2	27	Erect rigid, delicate branching
Microeciella sp.	Oncousoeciidae	6	35	Encrusting unilaminar

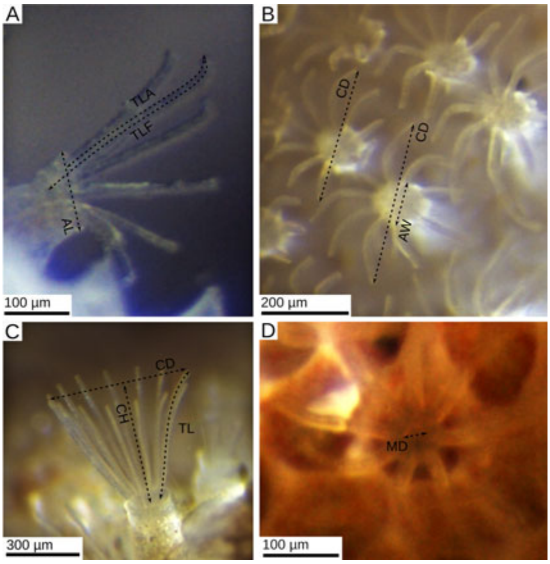

FIGURE 2. Four of the species examined in this study, showing some measured traits: A, *Idmidronea* sp. B, *Disporella pristis*. C, *Diaperoecia purpurascens*. D, *Favosipora rosea*. AL, aperture length; AW, aperture width; CD, diameter of the tentacle crown; CH, height of the tentacle crown; MD, mouth diameter; TL, tentacle length; TLA, length of the tentacle visible above the aperture; TLF, full tentacle length.

of the five soft-body traits (CD, CH, TN, TL, MD) and the zooid tube width. We put mean zooid widths (predictors) into the regression formulas and calculated predicted values of soft-body traits, which were later compared with actual measurements. To evaluate the predictions, we counted the number of testing values that fell into 95% predictive intervals of our modes and calculated the mean deviance between the predicted and testing values. Later, these measurements were included in the dataset. The resulting updated models are also reported here. We performed standard residuals checks on all regression models in this study: for normality (near-normality) of distribution, for patterns in residuals, and for influential observations.

Finally, we examined the levels of dissimilarity between bryozoan species from all three classes, taking into account several variables at once. To do this, we performed multivariate ordination in the form of nonparametric multidimensional scaling with Euclidean distances on a truncated hybrid dataset containing only complete measurement cases. To retain sufficient sample size, we had to restrict the list of variables to four: zooid tube width, crown diameter, and tentacle length and number. Further, whenever necessary, we complemented and/or averaged the cited measurements from different species of the same genus.

All statistical analyses were performed with R v. 3.4.4 (R Core Team 2018).

Results

Measured Zooid Parameters.—All characters examined here showed strong variability both within and between species (Table 2.1 and 2.2). Aperture length was equal to or exceeded the length of zooid tube opening at the orifice level, especially strongly in case of *Idmidronea*

Table 2. Part 1: Skeletal and tentacle crown characters measured in 13 cyclostomate species from New Zealand. All measurements are reported in micrometers (μm) as mean ± SD (sample size), while crown symmetry and curvature are given as the dominant value (its frequency/combined frequency of all other values). Coefficients of variation are reported for all measurements with sample size > 5. *See Fig. 1 for crown shapes. E, equitentacular; OT, obliquely truncated crown.

Species	Aperture length	Aperture width	Length of zooid tube opening at orifice	Width of zooid tube opening at orifice	Crown diameter	Crown height	Dominant symmetry*	Dominant curvature*
Cinctipora elegans	646 ± 155.7 (34) 0.24	588 ± 126.4 (46) 0.22	611 ± 115.3 (12) 0.19	411 ± 34.6 (10) 0.09	557 ± 94.8 (111) 0.17	309 ± 108.0 (56) 0.35	Equitentacular (53/36)	Scoop (61/42)
Diaperoecia purpurascens	192 ± 24.1 (53) 0.13	196 ± 36.6 (29) 0.19	195 ± 30.9 (54) 0.16	220 ± 64.9 (39) 0.30	584 ± 141.7 (90) 0.24	464 ± 130.2 (46) 0.28	Equitentacular (91/4)	Bell (61/27)
Diaperoecia sp.	156 ± 25.7 (7)† 0.18	148 ± 13.9 (15) 0.10	Same as aperture length	Same as aperture width	465 ± 103.0 (13) 0.23	318 ± 71.4 (10) 0.23	Obliquely truncated (11/0)	Trumpet (4/6)
Disporella pristis	143 ± 58.6 (28) 0.41	89 ± 9.8 (89) 0.11	102 ± 14.4 (48) 0.14	87 ± 10.1 (89) 0.12	355 ± 82.0 (148) 0.23	219 ± 63.8 (55) 0.29	Obliquely truncated (83/22)	Trumpet (80/35)
Disporella sp.	108 ± 14.1 (11) 0.13	93 ± 17.6 (28) 0.19	98 ± 15.2 (8) 0.16	80 ± 8.3 (8) 0.11	340 ± 55.9 (39) 0.17	204 ± 47.0 (23) 0.23	Obliquely truncated (17/6)	Trumpet (21/7)
Doliocoitis cyanea	101 ± 12.7 (23) 0.13	95 ± 8.1 (17) 0.09	100 ± 10.8 (21) 0.11	92 ± 10.8 (18) 0.12	304 ± 44.6 (33) 0.15	241 ± 41.6 (22) 0.17	Obliquely truncated (22/4)	Bell (26/1)
Favosipora rosea	133 ± 21.2 (86) 0.16	117 ± 14.9 (66) 0.13	125 ± 16.4 (91) 0.13	118 ± 14.2 (89) 0.12	324 ± 59.4 (159) 0.18	258 ± 79.6 (75) 0.31	Obliquely truncated (91/35)	Bell (90/15)
Hornera foliacea	106 ± 15.0 (46) 0.14	88 ± 10.5 (43) 0.12	103 ± 12.1 (25) 0.12	87 ± 9.4 (36) 0.11	287 ± 43.4 (133) 0.15	134 ± 19.4 (66) 0.15	Obliquely truncated (67/25)	Trumpet (62/24)
Hornera robusta	112 ± 19.3 (50) 0.17	100 ± 17.1 (40) 0.17	105 ± 17.8 (32) 0.17	99 ± 17.8 (36) 0.18	338 ± 57.0 (145) 0.17	173 ± 48.9 (66) 0.28	Obliquely truncated (97/13)	Trumpet (74/22)
Idmidronea sp.	174 ± 27.2 (7) 0.16	122 ± 13.2 (6) 0.11	107 ± 7.6 (18) 0.07	87 ± 10.6 (11) 0.12	354 ± 44.0 (20) 0,13	151 ± 42.6 (18) 0.29	Obliquely truncated (19/1)	Trumpet (12/8)
Microeciella sp.	82 ± 9.5 (21)† 0.12	71 ± 12.0 (24) 0.17	Same as aperture length	same as aperture width	324 ± 52.8 (30) 0.16	209 ± 51.7 (17) 0.25	Obliquely truncated (15/5)	Trumpet (17/6)
Platonea sp.	120 ± 16.6 (71)† 0.14	120 ± 16.6 (74) 0.14	Same as aperture length	same as aperture width	391 ± 70.7 (72) 0.18	267 ± 71.0 (65) 0.27	Obliquely truncated (36/35)	Trumpet (36/38)
Telopora lobata	134 ± 21.3 (55) 0.16	116 ± 21.0 (77) 0.18	127 ± 14.1 (43) 0.11	115 ± 20.9 (73) 0.18	323 ± 75.9 (65) 0.24	239 ± 57.6 (39) 0.24	Obliquely truncated (45/12)	Trumpet (17/35)

sp., *Cinctipora elegans*, and *Disporella pristis*. Aperture width was similar to the zooid tube width in all species except *C. elegans* and *Idmidronea* sp.

Characters of the tentacle crown tended to have somewhat greater dispersion than skeletal traits (Table 2). The smallest crown diameter was found in *Hornera foliacea* (287 ± 43.4 μm, 133), the largest in *Diaperoecia purpurascens* (584 ± 141.7 μm, 90), and there was variability of hundreds of micrometers within every species (Fig. 3A). Distribution of the crown heights was positively correlated with crown diameters ($r = 0.74$, $p \ll 0.001$; Table 3), with larger species having taller tentacle crowns. Exceptions to this rule included *Doliocoitis cyanea*, *Idmidronea* sp., and *H. foliacea*, which demonstrated no correlation between these two traits ($p > 0.5$); the latter two species also had unusually flattened tentacle crowns.

The aspects of crown shape varied between polypides (even from the same colony) in all studied species (Fig. 3B). Obliquely truncated crowns dominated in all species except the two largest ones: *C. elegans* and *D. purpurascens*; but equitentacular crowns were also present in all species but one (*Diaperoecia* sp.). Regardless of the symmetry of the crown, however, tentacles were usually deeply curved into a bell or trumpet shape with splayed tips. Scoop-shaped crowns represented an interesting exception to this trend, being fairly common in *Hornera robusta*, *H. foliacea*, *Platonea* sp., and *Telopora lobata*, and even dominant in *C. elegans*.

Tentacle parameters, too, demonstrated considerable variability (Table 2.2). The tentacle number was unstable in 10 out of 13 species (Fig. 3C). Full tentacle length was either larger than or similar to the tentacle length revealed above the aperture. In the majority of species the differences were relatively small (<15% of the tentacle length), and the tentacle crown protruded almost fully from the zooid opening, with the mouth slightly under or level with the aperture rim (e.g., Fig. 2A,C). In four species (*H. robusta*, *Diaperoecia* sp., *T. lobata*, and *D. purpurascens*), the length difference was

TABLE 2. PART 2: Characters of the tentacles and mouth. All measurements reported in µm as mean ± SD (sample size). Coefficients of variation are reported for all measurements with sample size > 5.

Species	Tentacle number	Full tentacle length	Length above aperture	Long tentacle length	Short tentacle length	Mouth diameter
Cinctipora elegans	16 ± 0.6 (86) 0.04	633 ± 53.1 (5) 0.09	352 ± 104.1 (70) 0.30	n/a (0)	579 (1)	48 ± 3.0 (5) 0.07
Diaperoecia purpurascens	15 ± 0.8 (73) 0.05	662 ± 184.1 (7) 0.29	505 ± 135.4 (58) 0.27	853 (1)	n/a (0)	46 ± 10.6 (8) 0.24
Diaperoecia sp.	9 ± 0.3 (11) 0.03	411 ± 89.3 (5) 0.23	334 ± 87.7 (12) 0.27	461 ± 94.2 (9) 0.21	324 ± 88.8 (8) 0.28	28 (2)
Disporella pristis	9 ± 0.1 (62) 0.01	262 ± 58.8 (31) 0.23	258 ± 54.5 (58) 0.21	392 ± 95.1 (19) 0.25	195 ± 47.8 (9) 0.25	23 ± 5.0 (38) 0.21
Disporella sp.	9 (17) n/a	263 ± 52.9 (5) 0.21	229 ± 47.3 (24) 0.21	282 ± 49.5 (20) 0.18	221 ± 38.6 (18) 0.18	21 ± 6.9 (13) 0.34
Doliocoitis cyanea	8 (14) n/a	262 ± 26.7 (16) 0.10	246 ± 37.9 (26) 0.16	301 ± 41.4 (22) 0.14	216 ± 35.1 (21) 0.16	22 ± 6.1 (4)
Favosipora rosea	8 (91) n/a	275 ± 59.7 (74) 0.22	262 ± 55.3 (80) 0.21	360 ± 108.1 (63) 0.30	235 ± 45.8 (34) 0.20	24 ± 3.6 (22) 0.16
Hornera foliacea	9 ± 0.2 (96) 0.02	198 ± 39.4 (14) 0.20	187 ± 30.7 (63) 0.17	233 ± 33.0 (42) 0.14	174 ± 26.3 (34) 0.15	25 ± 4.0 (26) 0.16
Hornera robusta	9 ± 0.1 (66) 0.01	246 ± 50.1 (6) 0.21	203 ± 44.3 (48) 0.22	288 ± 60.7 (56) 0.21	209 ± 57.4 (34) 0.28	25 ± 6.2 (39) 0.25
Idmidronea sp.	9 ± 0.8 (6) 0.09	239 ± 32.6 (5) 0.14	172 ± 46.0 (20) 0.27	313 ± 29.9 (9) 0.10	207 ± 44.8 (7) 0.22	n/a (0)
Microeciella sp.	8 ± 0.3 (12) 0.04	236 ± 44.0 (8) 0.19	218 ± 43.6 (22) 0.20	299 ± 68.5 (13) 0.23	214 ± 43.4 (13) 0.21	17 ± 0.6 (3)
Platonea sp.	9 ± 0.5 (22) 0.06	313 ± 54.0 (27) 0.17	293 ± 57.6 (72) 0.20	393 ± 94.5 (22) 0.24	264 ± 65.9 (15) 0.25	32 ± 10.4 (4)
Telopora lobata	10 ± 0.6 (64) 0.06	306 ± 60.1 (24) 0.20	246 ± 60.1 (57) 0.24	389 ± 62.5 (16) 0.16	217 ± 50.4 (8) 0.24	27 ± 4.8 (5) 0.18

between 15% and 25%. Finally in *Idmidronea* sp. and *C. elegans*, 28% and 44% of the tentacle length, respectively, was hidden below the aperture, potentially removed from generating feeding currents.

Our studied species differ in mouth diameter from 17 µm (±0.6, 3) in *Microeciella* sp. to 48 µm (±3.0, 5) in *C. elegans*, but differences were also present within species (Fig. 3D). Small sample sizes reflect the difficulty of measurement; more data could resolve the variation better.

Relationships between Zooid Parameters in Our Dataset.—The four skeletal parameters were strongly positively correlated with one another (Table 4), making it impossible to include all of them as independent predictors. Thus, we chose the width of the zooid tube near the orifice, rather than at the aperture, as a single measure that best approximates the internal diameter of the living chamber (after McKinney and Boardman 1985). The zooid chamber of most cyclostomates resembles a uniform, somewhat flattened cylinder that does not change shape near the orifice.

Measurements of the soft-body parts, that is, crown diameter and height, tentacle length and number, and mouth diameter, all demonstrated moderate to strong positive correlations with one another (0.67 to 0.80, all p-values $\ll 0.01$; Table 3) with a single exception: we found no correlation between tentacle number and mouth diameter.

Correlations between the zooid tube width and soft-body traits were weaker, although still positive and statistically significant (0.48 to 0.78, all p-values $\ll 0.01$; Table 3). For a more detailed analysis, we examined relationships between soft-body parameters and tube width separately for each species. The number of available observations was not always sufficient for linear modeling within each species, but when it was, we often found that tube width predicted parameters of the feeding apparatus poorly or not at all (adjusted R^2 between 0 and 0.37), with regression coefficients not statistically significant (Fig. 4).

When species data were pooled, tube width became a somewhat better predictor of most soft-body traits (adjusted R^2 between 0.24

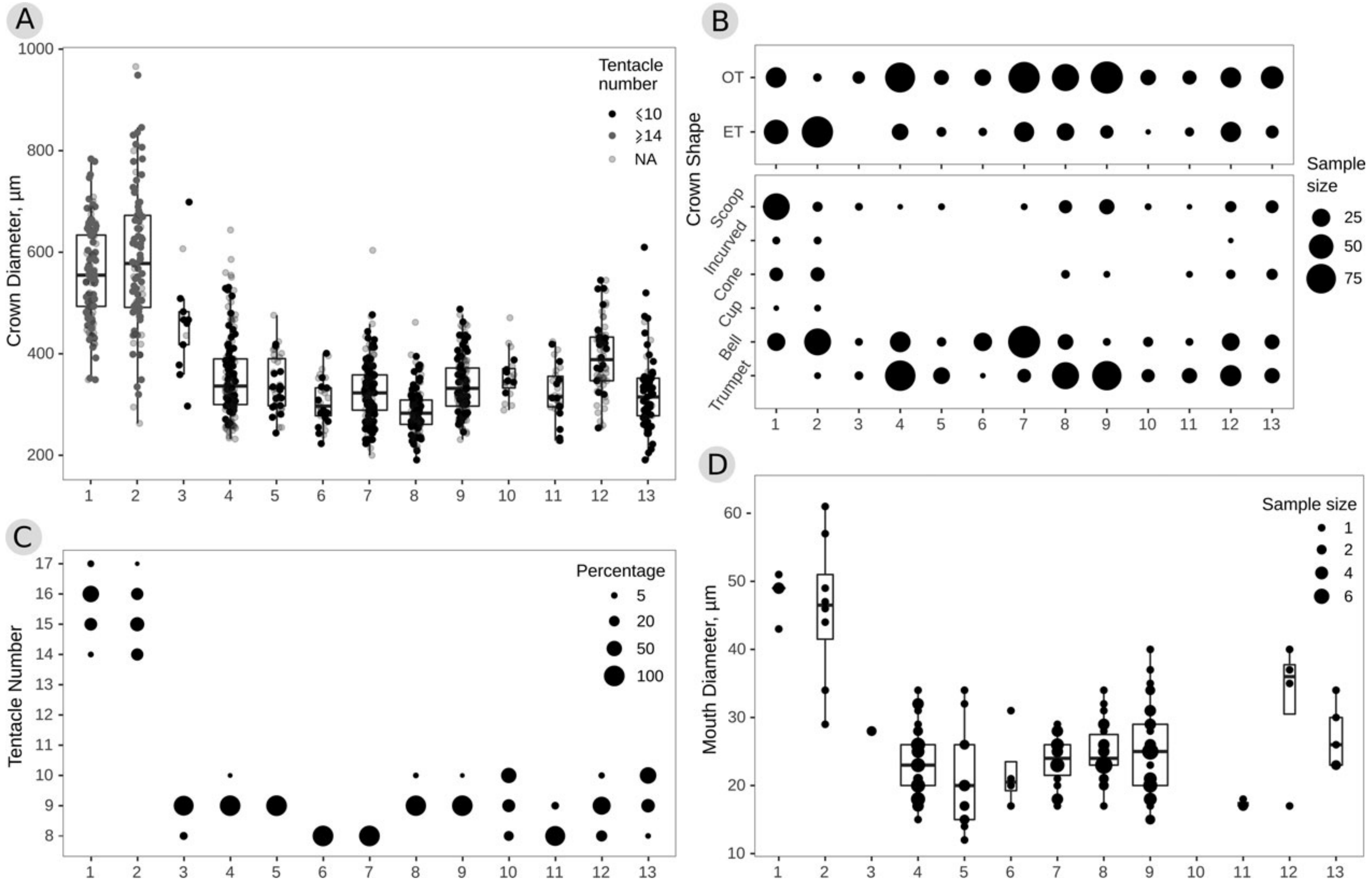

FIGURE 3. Descriptive plots of selected polypide parameters: A, Tentacle crown diameter. B, Tentacle crown shape and symmetry. C, Tentacle number. D, Mouth diameter. On every plot the x-axis lists the studied species in alphabetical order: 1, *Cinctipora elegans*; 2, *Diaperoecia purpurascens*; 3, *Diaperoecia* sp.; 4, *Disporella pristis*; 5, *Disporella* sp.; 6, *Doliocoitis cyanea*; 7, *Favosipora rosea*; 8, *Hornera foliacea*; 9, *Hornera robusta*; 10, *Idmidronea* sp.; 11, *Microeciella* sp.; 12, *Platonea* sp.; 13, *Telopora lobata*. ET stands for equitentacular crown, OT, for obliquely truncated lophophore shape as depicted on Fig. 1.

TABLE 3. Pearson's product-moment correlations between soft-body characters for 13 measured species combined (based on specimen measurement pairs). The *p*-values were corrected with the Holm method (1979).

	Zooid tube width	Crown diameter	Crown height	Tentacle length	Tentacle number
Crown diameter	0.53 ($p \ll 0.01$, df = 361)				
Crown height	0.64 ($p \ll 0.01$, df = 142)	0.74 ($p \ll 0.01$, df = 533)			
Tentacle length	0.48 ($p \ll 0.01$, df = 71)	0.80 ($p \ll 0.01$, df = 192)	0.88 ($p \ll 0.01$, df = 162)		
Tentacle number	0.78 ($p \ll 0.01$, df = 240)	0.80 ($p \ll 0.01$, df = 532)	0.60 ($p \ll 0.01$, df = 186)	0.79 ($p \ll 0.01$, df = 75)	
Mouth diameter	0.51 ($p \ll 0.01$, df = 80)	0.67 ($p \ll 0.01$, df = 108)	n/a	0.55 ($p > 0.1$, df = 5)	0.78 ($p \ll 0.01$, df = 117)

TABLE 4. Pearson's product-moment correlations between skeletal traits for 13 measured species combined (based on specimen measurement pairs). The *p*-values were corrected with the Holm method (1979).

	Length of zooid tube opening	Zooid tube width	Aperture length
Zooid tube width	0.92 ($p \ll 0.01$, df = 311)		
Aperture length	0.91 ($p \ll 0.01$, df = 337)	0.81 ($p \ll 0.01$, df = 274)	
Aperture width	0.95 ($p \ll 0.01$, df = 243)	0.95 ($p \ll 0.01$, df = 346)	0.94 ($p \ll 0.01$, df = 292)

and 0.42, all $p \ll 0.01$. Table 5). Regression lines for each character pair are given in Figure 4. Unlike other dependent variables, the relation between tube width and tentacle number in our dataset could not be modeled with a linear formula. Residuals from a regression test revealed violations of assumptions: severe divergence from normality and pronounced patterns in the residuals.

Relationships between Zooid Parameters in a Hybrid Dataset.—We performed an analogous set of regression tests on a hybrid dataset that combined published data with our measurements (Figs. 5–7). *Cinctipora elegans* was removed from this dataset for reasons of biological (as having unusual zooid shape) as well as statistical nature (as an outlier with extreme leverage). Unlike the dataset containing only our measurements, tentacle number data from a combined dataset were successfully analyzed, and no violations of the assumptions were detected. We found that models including three predictors, that is, zooid tube width, class, and the interaction term, achieved the best fit (Table 5). This held true for all dependent variables except crown height, because there were too few available observations.

Because our formulas are intended to be used for predictions of fossil bryozoans, they may never be tested against the actual soft-body measurements. As the next best alternative, we tested the predictive power of the models by measuring photographs of nine unidentified cyclostomate species and comparing the test values with the values predicted by the models. In most cases (22 out of 27), the test values did not overstep the 95% predictive intervals of the regressions (insets in Figs. 5–7). The new measurements were adequately predicted by models describing the mouth diameter and tentacle number, but not crown parameters. The average of the deviations of real against predicted values was very close to zero (−0.2, 3) for tentacle number and mouth diameter, indicating a uniform spread of the data points around the regression line. For crown diameter, crown height, and tentacle length, however, the mean deviations differed from zero substantially (72, −38, and −22, respectively), indicating that test values appeared predominantly either above or below the regression line.

With the test values added into the hybrid dataset, we calculated updated regression models for all three bryozoan classes (Table 6A). We also had a sufficient number of observations to perform the regression analyses on the datasets containing only stenolaemates (Table 6B). Updated linear models, restricted

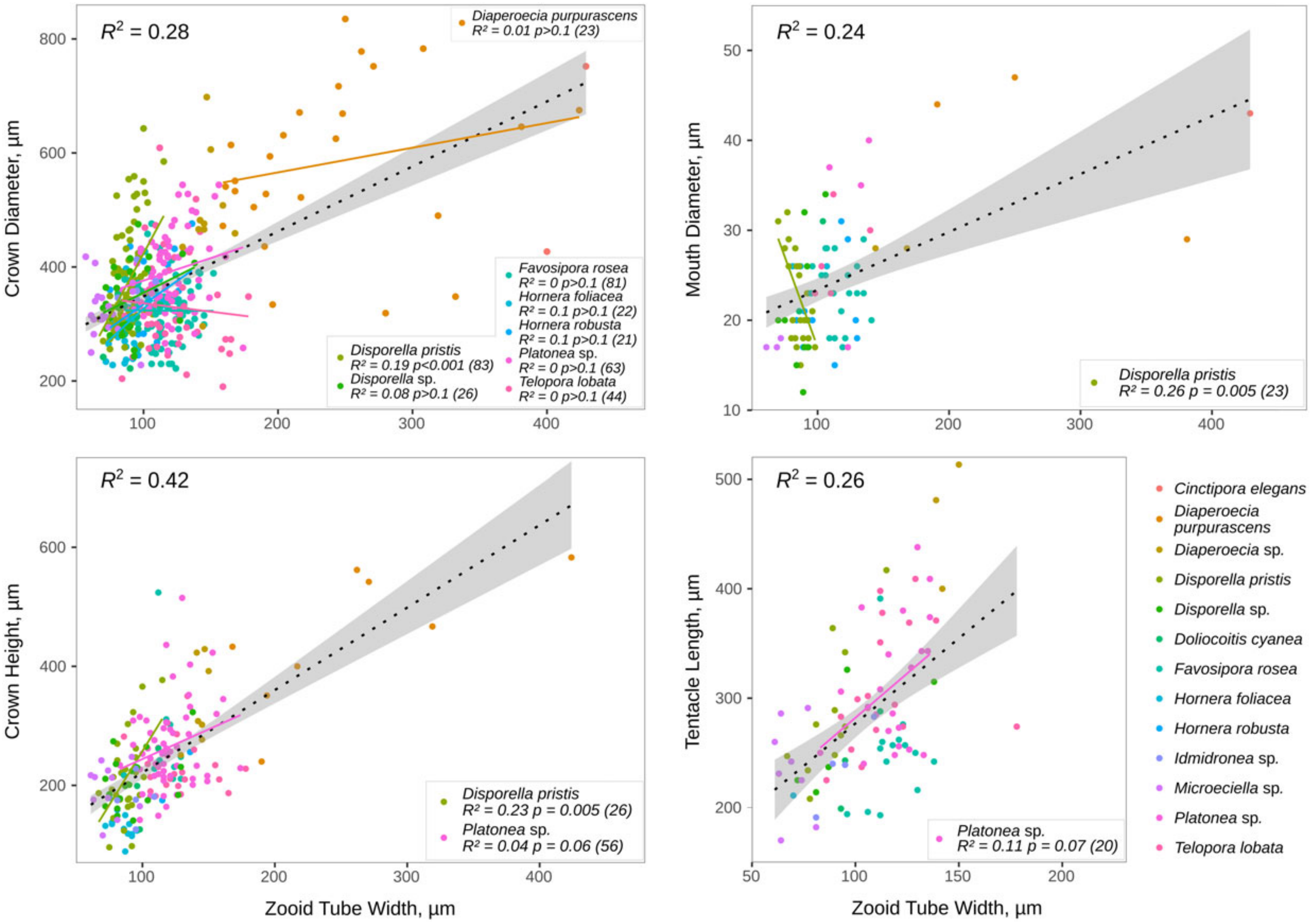

FIGURE 4. Linear regressions showing relationships between dependent variables (tentacle crown diameter, height, mouth diameter, and tentacle length) with a single independent variable: zooid tube width. Regression lines are plotted both for individual species (colored) and for all species pooled (dotted black line with confidence interval shown as a gray band).

TABLE 5. Details of regression analyses for zooid tube width (predictor) and soft-body characters (responses). Models are reported in the form: Intercept + Slope*Predictor. R^2 values are given as adjusted R^2/predicted R^2. ***p-value ≪ 0.001.

	Crown diameter	Crown height	Tentacle length	Tentacle number	Mouth diameter
Coefficients: our dataset	$234.5 + 1.14x^{***}$	$82.9 + 1.39x^{***}$	$121.4 + 1.56x^{***}$	n/a (assumptions violated)	$16.9 + 0.06x^{***}$
Diagnostics	$R^2 = 0.28/0.26$ $S = 86$; df = 423	$R^2 = 0.42/0.41$ $S = 67$; df = 185	$R^2 = 0.26/0.22$ $S = 59$; df = 88	n/a	$R^2 = 0.24/0.17$ $S = 6$; df = 88
Coefficients: hybrid dataset	$150.1 + 1.85x^{***}$	$168.3 + 1.2x^{***}$	$16.3 + 2.7x^{***}$	$4.8 + 0.042x^{***}$	$4.4 + 0.19x^{***}$
Diagnostics	$R^2 = 0.89/0.81$ $S = 145$; df = 64	$R^2 = 0.72/0.54$ $S = 152$; df = 22	$R^2 = 0.76/0.68$ $S = 111$; df = 64	$R^2 = 0.93/0.91$ $S = 3$; df = 78	$R^2 = 0.91/0.77$ $S = 8$; df = 44

to Stenolaemata, often demonstrated reduced fitness and lower predictive power compared with models based on all bryozoan classes (compare R^2 values in Table 6A,B), but they were free of nonlinear patterns and influential observations (Cook's distances < 0.8).

Finally, to visualize the amount of dissimilarity between bryozoan species using four variables at once, we performed a nonmetric multidimensional scaling (MDS). The resulting scaling had a low enough stress (0.113) to allow interpretation of the relative positions of data points on the plot (Fig. 8). Overall, the density of the data points indicate that bryozoans have relatively small range of proportions. The point cloud of the cyclostomates is smaller and overlaps considerably with that of gymnolaemates (Cheilostomata + Ctenostomata), indicating that the former group occupies only a part of the morphospace available to the latter.

Discussion

This is the first detailed and coordinated report of morphometry in the cyclostomate Bryozoa. Among the cystid and polypide characteristics measured in this study, crown and tentacle traits are of the most interest.

Crown diameters, measured here, fall between 190 and 956 μm (individual measurements), with species means ranging from 287 to 584 μm. This agrees with previous studies (Ryland 1975; Winston 1977, 1978, 1979; Shunatova and Ostrovsky 2001) and fits with the notion of the cyclostomates being generally smaller than gymnolaemates (60–1280 μm [species means]; data from Ryland 1975, 1976; Winston 1977, 1978, 1979; Buss 1979; Herrera and Jackson 1992; Shunatova and Ostrovsky 2001).

In gymnolaemates and phylactolaemates, shorter tentacles tend to be straight, while long ones are usually curved: bent inward or outward or S-shaped (Ryland 1976; Sanderson et al. 2000; Tamberg and Shunatova 2017). By contrast, in cyclostomates, we did not see any relation between tentacle curvature and length. Cone-shaped crowns comprising straight tentacles were equally rare in species with short and long tentacles (Fig. 3B), and both within and across species, straight tentacles were not significantly shorter than curved ones.

Interestingly, in some cyclostomate species, an increase in tentacle length does not always correspond to an increase in crown height. For instance, *H. foliacea* and *Idmidronea* sp. have rather flattened, splayed tentacle crowns (regression slopes did not differ from zero). By contrast, in gymnolaemates, the proportions of the tentacle crowns are very conservative, even as their sizes vary (Ryland 1975).

We used the formula TD = π*CD/TN to roughly estimate intertentacular tip distances (TD) from our measurements by reconstructing crown circumference from diameter (CD) and dividing it by the number of tentacles (TN). Admittedly, this approach does not take into account possible oval rather than circular shapes of the crown edge or uneven spacing of the tentacle tips. These imperfections, however, would lead to underestimated, rather than overestimated, intertentacular tip distances. Pooled, these distances in the studied Cyclostomatida varied from 55 to 240 μm (individual measurements), with medians ranging

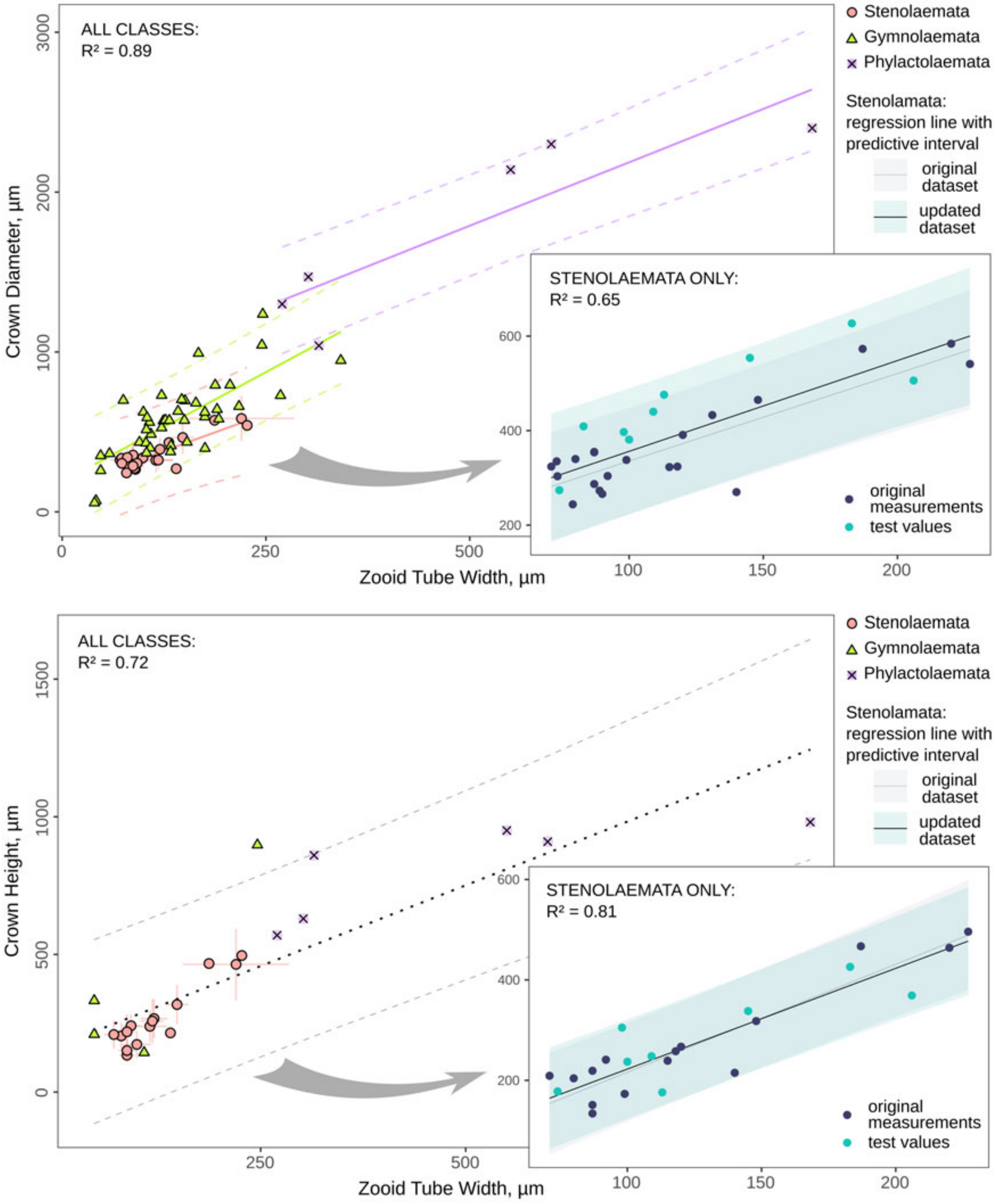

FIGURE 5. Linear regressions based on a hybrid dataset uniting our measurements and data from published sources. Presented variables include tentacle crown diameter and height plotted against zooid tube width. All regression lines are presented together with their 95% predictive intervals. Two insets represent correspondence between original models and models updated by the addition of the test values.

from 99 to 160 µm (13 species). It was not surprising to find such relatively large values, because many measurements come from obliquely truncated tentacle crowns with uneven tentacle lengths. We expected to see smaller intertentacular tip distances among

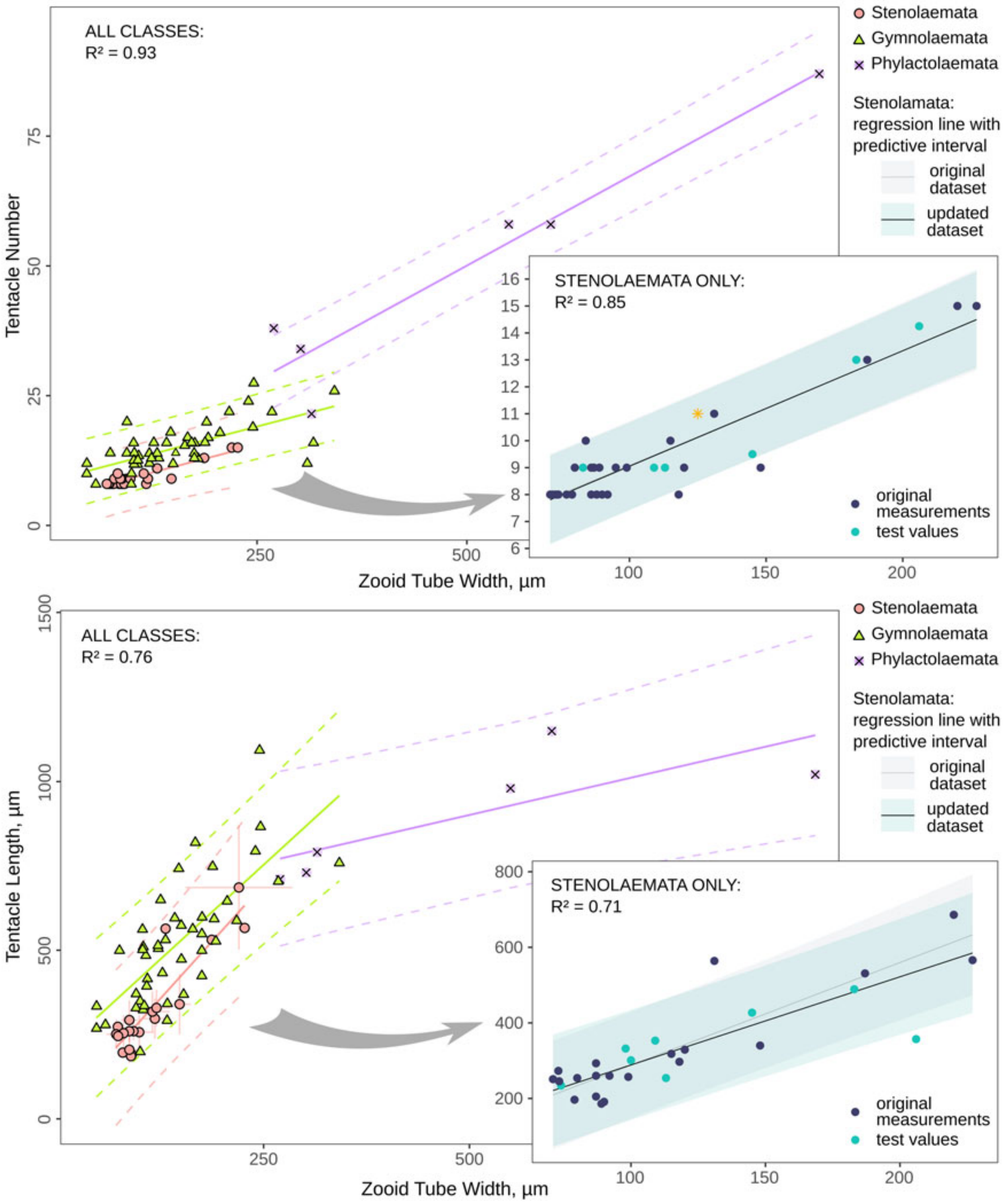

FIGURE 6. Linear regressions based on a hybrid dataset uniting our measurements and data from published sources. Variables include tentacle length and number plotted against zooid tube width. All regression lines are presented together with their 95% predictive intervals. Two insets represent stenolaemate-specific correspondence between original models and models updated by the addition of the test values. An asterisk in the upper inset represents an Ordovician trepostome *Tetratoechus crassimuralis* (Boardman and McKinney 1976).

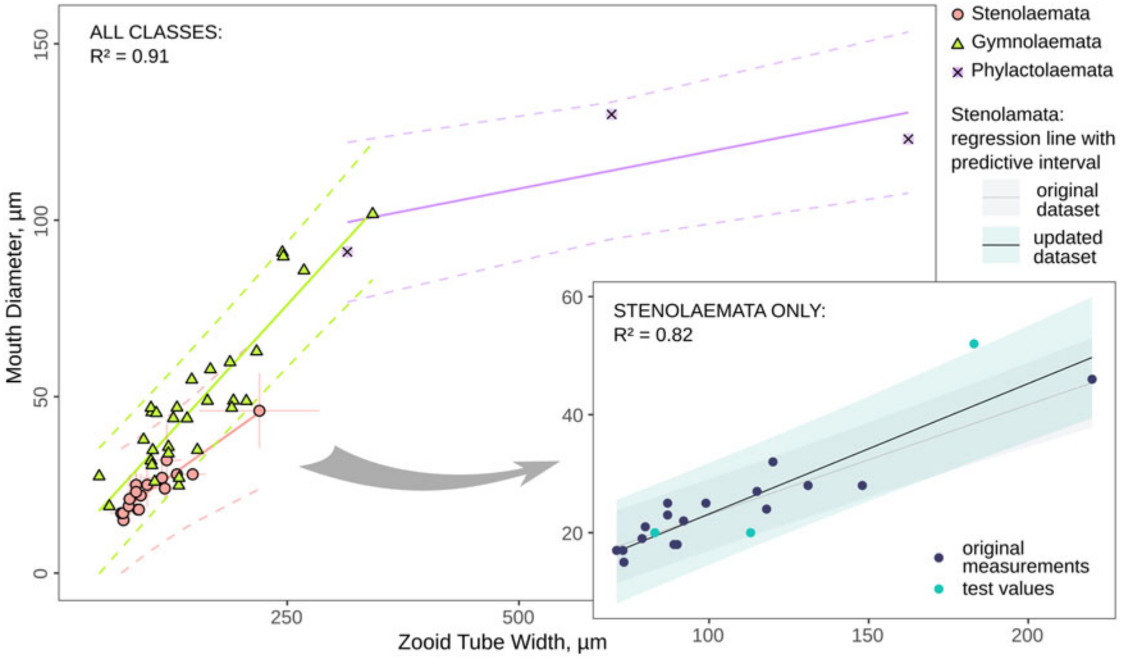

FIGURE 7. Linear regressions (mouth diameter vs. zooid tube width) based on a hybrid dataset uniting our measurements and data from published sources. All regression lines are presented together with their 95% predictive intervals. An inset represents correspondence between original models and models updated by the addition of the test values.

strictly equitentacular crowns, and indeed the distances stabilized between 100 and 125 µm. This interval agrees with distances reported for Gymnolaemata, which hold tentacle tips about 110 (77–134) µm apart (Ryland 1975). A distance of 140 µm and above is considered extreme for gymnolaemates (Riisgård and Manríquez 1997; Sanderson et al. 2000).

Among tentacle crown shapes, obliquely truncated crowns dominated in 10 of 13 examined species (except *D. purpurascens*, *C. elegans*, and *Platonea* sp.), while in the study by Winston (1978), 27 gymnolaemate species had equitentacular crowns and in 24 species at least some polypides were non-equitentacular. This suggests a much stronger presence of obliquely truncated crowns among cyclostomates, although the sample size is limited.

Winston (1981) and other authors (Lidgard 1981; Pratt 2004, 2008; von Dassow 2006) linked asymmetrical crown shapes with increased velocity of feeding currents, which is especially important in expelling already-filtered water away from the colony. Obliquely truncated lophophores often flank the excurrent chimneys in both gymnolaemates and cyclostomates (Cook 1977; Winston 1981; Shunatova and Ostrovsky 2002), but in our study they seemed even more widespread, especially among species with few tentacles. The prevalence of non-symmetrical crowns, together with larger intertentacle tip distances, may mean that tentacles are partly independent. But, as the number of tentacles increases, cyclostomates approach cheilostomates in the crown shape, intertentacle tip distance, and thus crown proportions. Is it possible that asymmetrically shaped crowns give specific advantage to smaller polypides?

Tentacle number varied considerably in some of the examined species, while remaining stable in others, both states having been found before in cyclostomates and gymnolaemates alike (e.g., Borg 1926; Rogick 1949; Ryland 1975; Winston 1977; Schäfer 1985; Thorpe et al. 1985; McKinney 1991; Ryland and Hayward 1991). While changes in the interspecific tentacle number in Gymnolaemata were connected to ecological parameters, such as temperature (Amui-Vedel et al. 2007), presence or absence of competition (Thorpe et al. 1985),

TABLE 6. Details of a repeated regression analyses for zooid tube width (predictor) and soft-body parameters (responses) of bryozoan classes, based on a hybrid dataset updated to include the test values. Models are reported in the form Intercept + Slope*Predictor. ***p-value ≪ 0.001.

	Crown diameter	Crown height	Tentacle length	Tentacle number	Mouth diameter
A. Models based on all three classes					
Coefficients: Stenolaemata	$163.9 + 1.9x^{***}$	$154.5 + 1.2x^{***}$	$55.3 + 2.3x^{***}$	$4.8 + 0.043x^{***}$	$1.1 + 0.22x^{***}$
Coefficients: Gymnolaemata	$187.7 + 2.7x^{***}$		$194.6 + 2.23x^{***}$	$8.4 + 0.042x^{***}$	$4.0 + 0.29x^{***}$
Coefficients: Phylactolaemata	$775.2 + 2.0x^{***}$		$619.6 + 0.56x^{***}$	$5.7 + 0.089x^{***}$	$83.2 + 0.05x^{***}$
Diagnostics	$R^2 = 0.89/0.81$ $S = 139$; df = 73	$R^2 = 0.73/0.57$ $S = 134$; df = 31	$R^2 = 0.76/0.69$ $S = 108$; df = 72	$R^2 = 0.93/0.91$ $S = 3$; df = 84	$R^2 = 0.90/0.77$ $S = 8$; df = 47
B. Models based on Stenolaemata only					
Coefficients: Stenolaemata	$163.9 + 1.9x$	$21.8 + 2.0x$	$55.3 + 2.3x$	$4.8 + 0.043x$	$1.1 + 0.22x$
Diagnostics	$R^2 = 0.65/0.61$ $S = 64$; df = 28	$R^2 = 0.81/0.78$ $S = 46$; df = 21	$R^2 = 0.71/0.65$ $S = 69$; df = 26	$R^2 = 0.85/0.84$ $S = 0.8$; df = 32	$R^2 = 0.82/0.73$ $S = 4$; df = 18

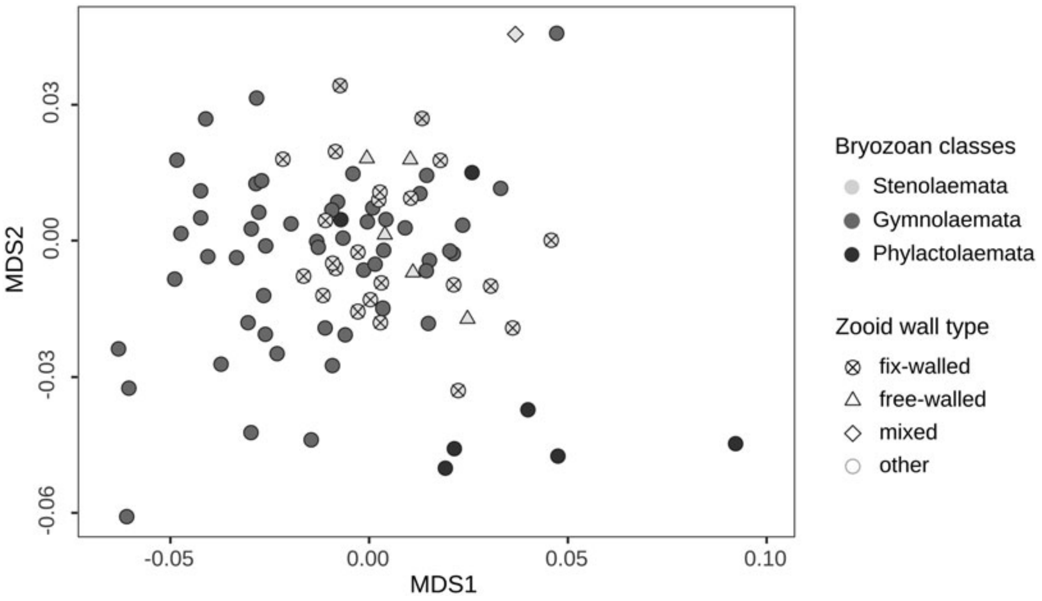

FIGURE 8. Results of nonmetric MDS plotted in two main axes (stress = 0.122). Variables used in the analysis include zooid tube width, crown diameter, and tentacle length and number.

and feeding conditions (Jebram 1973), little is known about the connection between tentacle number and ecological conditions in Cyclostomatida. It seems very likely, however, that such connections exist.

Cyclostomates are often reported as having the smallest feeding apparatus in the phylum, with tentacles ranging from 150 to 450 µm in length (Borg 1926; Winston 1978; McKinney 1991). Our results show that in some species tentacles can be much larger: up to 700 (mean length within a species) or 900 µm (individual measurements). Because all measurements were made from extended polypides, we can conclude that in Cyclostomatida the polypides feed at very different sizes and start feeding while very small. Indeed, if a definitive "adult" zooid size exists, cyclostomates start feeding long before reaching it (Silén and Harmelin 1974).

The ability to start protruding (and presumably feeding) while still developing and growing is also seen in phylactolaemate polypides (Y. Tamberg personal observations). Cyclostomates and freshwater bryozoans are thus in stark contrast with cheilostomates, which only begin feeding when fully grown (Marcus 1926), because their polypides attain definitive size at the same time as the opercular apparatus becomes functional.

The full length of the tentacles in our measurements was equal to or somewhat larger than the length of the tentacle parts protruding above the aperture. Theoretical considerations point at free-walled species as potentially having smaller or no difference between full and revealed tentacle lengths, because they have a shared hypostegal cavity (Borg 1926), which provides an additional reservoir for body cavity fluid and may increase protrusibility of tentacles (Taylor 1981). Surprisingly, we found no evidence to support this view. There was no connection between zooid wall type and differences between full tentacle length and length above the aperture. Indeed, *C. elegans*, a species with mixed free- and fixed-walled zooids, had the most deeply set polypides. Our nonmetric MDS graph also did not reflect the grouping of the cyclostomates based on zooid wall type (Fig. 8).

Overall, within-species regressions based on our measurements show that characters of soft-body morphology are often independent from skeletal parameters (R^2 between 0 and 0.26). Although it seemed likely that increased level of detail would improve the predictive power of these models, nothing was gained through it. We found that species-specific morphometric traits are poorly connected across the skeleton–soft body divide and the natural intracolonial and intraspecific variability of polypide characteristics is very strong.

Analyses of the combined dataset with all classes incorporated were much more helpful in terms of explaining the values of the dependent variables. Compared with the models based only on our measurements, all models of the combined dataset demonstrated improved adjusted R^2 (i.e., increased amount of explained variance). In the cases of tentacle length and mouth diameter, the standard error of regression also improved (i.e., decreased), while for crown parameters it increased. Overall, however, the combined models are better at explaining variance.

The apparent advantage of the regression models based on a combined dataset, compared with solely our own measurements is mostly due to the considerable variability found within each species is collapsed into a single number—its central tendency, the mean. Thus, it is only means that these models explain and predict. The true variability remains hidden, and if there are smaller-scale relationships between soft-body and skeletal parameters acting within species, we failed to detect them.

Still, these models performed only adequately in predicting measurements (5 out of 27 test values fell outside the 95% predictive interval). Even worse, additional data points from the testing dataset altered the coefficients of the models. Undoubtedly, input of more species into the dataset would result in further changes. Therefore, we recommend caution while using our formulas for interpolations, and doubly so for extrapolations. Nevertheless, recognizing the need for predictions in the practical work of paleontologists and paleoecologists, we propose the following: for each value of independent variable (zooid tube width), report not only the predicted value of the response variable, but also the upper and lower boundaries of the appropriate 95% predictive interval (for an easy approximation of this interval, multiply the residual standard error S of the regression by 1.96).

In the past, several studies attempted to determine the nature of and generate formulas describing the relationship between the skeletal and polypide characters. Skeletal traits used in these studies as independent variables were aperture/orifice/living chamber width and distance to the nearest neighboring zooid. Among soft-body traits, tentacle number is the most commonly used, with crown and mouth diameter addressed as distant seconds (Winston 1981; McKinney and Jackson 1991).

Presence of a positive, moderately strong, and statistically significant relationship between polypide and skeletal traits was established in a number of studies (e.g., Winston 1977, 1981; Schäfer 1985; McKinney and Jackson 1991) and confirmed in the present analysis. This in itself may be sufficient for some applications. Knowing that zooid tube width reliably correlates with polypide dimensions is sufficient to confidently compare skeletal remains from different bryozoan fossil communities, compare stenolaemate faunas (Reid and Tamberg 2019), and look for size distributions between stenolaemate orders.

In other situations it may be helpful to reconstruct the actual dimensions of the tentacle crown, because tentacle parameters (length and number) tie into food size and feeding parameters such as clearance rate (Strathmann 1973) and particle speed (Best and Thorpe 1986). The latter can tell more about ecological roles and interactions between the members of benthic communities and, potentially, about the surrounding conditions. Thus, it may be important to choose the most suitable regression formula for specific reconstructions.

Existing regressions (e.g., in Winston 1981; McKinney and Boardman 1985) and present data cover a similar zooid tube size range from ~60 to ~275 μm and include large living species (*C. elegans* and *D. purpurascens* measured by us, and *Heteropora* sp. from a hybrid dataset). The model coefficients themselves, however, differ notably both between studies and between our own analyses. We hesitate to single out any one formula as the best, because they all have their limitations, but we believe that ones that include the greatest number of species (i.e., updated combined dataset) are probably more suited for predicting soft-body parts from skeletal remains.

Necessarily, these predictions are additionally limited by the fact that only one order from the class Stenolaemata has survived to the present day. We may never know how deep were the differences in the soft-part morphology of the stenolaemate orders, and using one to predict the others carries inherent risk. However, some fossils retain what look like tentacles or tentacle-related structures that can be counted. For instance, 11 preserved tentacle remains were found in a zooid of the Ordovician trepostome *Tetratoechus crassimuralis* (Boardman and McKinney 1976: Plate 13, Fig. 1). When plotted, it fell close to the regression line, supporting our model (inset in Fig. 6).

We also wish to point out the considerable interspecies variability within the Stenolaemata. In our nonmetric MDS plot (Fig. 8) cyclostomates occupied a substantial area in a multidimensional morphospace despite being outnumbered 10 to 1 by the flourishing modern gymnolaemates in the sea (543 vs. 5240 species; Bock and Gordon 2013) and 2 to 1 in the dataset ($n = 29$ vs. $n = 52$). The high intra- and interspecific variability of the modern stenolaemates revealed in this study necessitates proper respect for the underlying uncertainties of predictive modeling in this group.

Acknowledgments

We are most grateful to K. Currie (National Institute of Water and Atmospheric Research, Wellington, New Zealand) for generously sharing many sampling opportunities. We also wish to thank the staff at the Portobello Marine Laboratory (R. Pooley, L. Groenewegen) and the master and crew of RV *Polaris II* (B. Dickson, E. Kenton), University of Otago. Gratitude is due to C. Reid (Canterbury University) for discussion and to P. Batson (University of Otago) for providing valuable comments on the article. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Literature Cited

Amui-Vedel, A. M., P. J. Hayward, and J. S. Porter. 2007. Zooid size and growth rate of the bryozoan *Cryptosula pallasiana* Moll in relation to temperature, in culture and in its natural environment. Journal of Experimental Marine Biology and Ecology 353:1–12.

Batson, P. B., and P. K. Probert. 2000. Bryozoan thickets off Otago Peninsula. Ministry of Fisheries, Wellington.

Best, M. A., and J. P. Thorpe. 1986. Feeding current interactions and competition for food among the bryozoan epiphytes of *Fucus serratus*. Marine Biology 93:371–375.

Boardman, R. S., and F. K. McKinney. 1976. Skeletal architecture and preserved organs of four-sided zooids in convergent genera of Paleozoic Trepostomata (Bryozoa). Journal of Paleontology 50:25–78.

Bock, P. E., and D. P. Gordon. 2013. Phylum Bryozoa Ehrenberg, 1831. Zootaxa 3703:67–74.

Borg, F. 1926. Studies on recent cyclostomatous Bryozoa. Zoologiska Bidrag från Uppsala 10:181–50.

Borg, F. 1944. The stenolaematous Bryozoa. Further Zoological Results of the Swedish Antarctic Expedition 1901–1903 3:1–16.

Buss, L. W. 1979. Bryozoan overgrowth interactions—the interdependence of competition for space and food. Nature 281:475.

Cook, P. L. 1977. Colony-wide water currents in living Bryozoa. Cahiers de Biologie Marine 18:31–47.

Gordon, D. P., and P. D. Taylor. 2001. New Zealand Recent Densiporidae and Lichenoporidae (Bryozoa: Cyclostomata). Species Diversity 6:243–290.

Gordon, D. P., P. D. Taylor, and F. P. Bigey. 2009. Phylum Bryozoa—moss animals, sea mats, lace corals. Pp. 271–297 *in* D. P. Gordon, ed. New Zealand inventory of biodiversity, Vol. 1. Kingdom Animalia: Radiata, Lophotrochozoa, Deuterostomia. Canterbury University Press, Christchurch.

Herrera, A., and J. B. C. Jackson. 1992. Environmental versus taxonomic variation in lophophore morphology of Panamanian cheilostome bryozoans. Marine Biology 112:99–106.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Hutton, F. W. 1873. Catalogue of the marine Mollusca of New Zealand with diagnoses of the species. Didsbury, Wellington.

Hutton, F. W. 1877. Corrections and additions to the list of Polyzoa in the Catalogue of the Marine Mollusca of New Zealand (1873). Transactions and Proceedings of the New Zealand Institute 9:358–361.

Inkscape Project. 2011. Inkscape 0.48.1. http://www.inkscape.org, accessed 9 March 2020.

Jebram, D. 1973. Preliminary observations of the influences of food and other factors on the growth of Bryozoa with the description of a new apparatus for cultivation of sessile plankton feeders. Kieler Meeresforschungen 29:50–57.

Lidgard, S. 1981. Water flow, feeding, and colony form in an encrusting cheilostome. Pp. 135–142 *in* G. P. Larwood and C. Nielsen, eds. Recent and fossil Bryozoa. Olsen & Olsen, Fredenborg, Denmark.

MacGillivray, P. H. 1869. Descriptions of some new genera and species of Australian Polyzoa: to which is added a list of species found in Victoria. Transactions and Proceedings of the Royal Society of Victoria 9:126–148.

MacGillivray, P. H. 1883 Descriptions of new, or little known, Polyzoa. Part IV. Transactions and Proceedings of the Royal Society of Victoria 19:287–293.

MacGillivray, P. H. 1884. Descriptions of new, or little known, Polyzoa. Part VI. Transactions and Proceedings of the Royal Society of Victoria 20:126–128.

Marcus, E. 1926. Bryozoa. Pp. 1–100 *in* G. Grimpe and E. Wagler, eds. Die Tierwelt der Nord- und Ostsee. Part 7, c-1. Akademische Verlagsgesell, Leipzig.

McKinney, F. K. 1990. Feeding and associated colonial morphology in marine bryozoans. Critical Reviews in Aquatic Sciences 2:255–280.

McKinney, F. K. 1991. Colonial feeding currents of *Eximonea atlantica* (Cyclostomata). *In* F. P. Bigey, ed. Bryozoaires actuels et fossiels: Bryozoa living and fossil. Bulletin de la Société des Sciences Naturelles de l'Ouest de la France, Mémoire Hors Série 1:263–270.

McKinney, F. K., and R. S. Boardman. 1985. Zooidal biometry of Stenolaemata. Pp. 193–203 *in* C. Nielsen and G. P. Larwood, eds. Bryozoans: Ordovician to Recent. Olsen & Olsen, Fredensborg, Denmark.

McKinney, F. K., and J. B. Jackson. 1991. Bryozoan evolution. University of Chicago Press, London.

Mukai, H., K. Terakado, and C. G. Reed. 1997. Bryozoa. Pp. 45–206 *in* F. W. Harrison, ed. Microscopic anatomy of invertebrates. Vol 13. Wiley-Liss, New York.

Nielsen, C., and K. J. Pedersen. 1979. Cystid structure and protrusion of the polypide in *Crisia* (Bryozoa, Cyclostomata). Acta Zoologica 60:65–88.

Nielsen, C., and H. U. Riisgård. 1998. Tentacle structure and filter-feeding in *Crisia eburnea* and other cyclostomatous bryozoans, with a review of upstream-collecting mechanisms. Marine Ecology Progress Series 168:163–186.

Pratt, M. C. 2004. Effect of zooid spacing on bryozoan feeding success: is competition or facilitation more important? Biological Bulletin 207:17–27.

Pratt, M. C. 2008. Living where the flow is right: How flow affects feeding in bryozoans. Integrative and Comparative Biology 48:808–822.

Ramalho, L. V., G. Muricy, and P. D. Taylor. 2009. Cyclostomata (Bryozoa, Stenolaemata) from Rio de Janeiro State, Brazil. Zootaxa 2057:32–52.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Reid, C., and Y. Tamberg. 2019. Order level trophic structuring across Permian Gondwanan fauna. P. 62 *in* K. Zágoršek, ed. 18th International Bryozoology Association Conference (Liberec), Abstracts. Technická Univerzita Liberci, Liberec, Czech Republic.

Riisgård, H. U., and P. Manríquez. 1997. Filter-feeding in fifteen marine ectoprocts (Bryozoa): particle capture and water pumping. Marine Ecology Progress Series 154:223–239.

Rogick, M. D. 1949. Studies on marine Bryozoa. IV. *Nolella blakei* n. sp. Biological Bulletin 97:158–168.

Ryland, J. S. 1967. Crisiidae (Polyzoa) from western Norway. Sarsia 29:269–282.

Ryland, J. S. 1970. Bryozoans. Hutchinson University Library, London.

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pp. 363–393 *in* H. Barnes, ed. Proceedings of the 9th European Marine Biology Symposium. Aberdeen University Press, Oban, Scotland.

Ryland, J. S. 1976. Physiology and ecology of marine bryozoans. Advances in Marine Biology 14:285–443.

Ryland, J. S., and P. J. Hayward. 1991. Marine flora and fauna of the Northeastern United States: erect Bryozoa. National Oceanic and Atmospheric Administration technical report NMFS series, Vol. 99. U.S. Department of Commerce, Springfield, Mo.

Sanderson, W. G., J. P. Thorpe, and A. Clarke. 2000. Aspects of structure and function in the feeding of the Antarctic cheilostomate bryozoan, *Himantozoum antarcticum* (Calvet). Pp. 355–364 *in* A. Herrera Cubilla and J. B. C. Jackson, eds. Proceedings of the 11th International Bryozoology Association Conference. Smithsonian Tropical Research Institute, Balboa, Panama.

Schäfer, P. 1985. Significance of soft part morphology in the classification of recent tubuliporoid cyclostomes. Pp. 273–284 *in* C. Nielsen and G. P. Larwood, eds. Bryozoa: Ordovician to Recent. Olsen & Olsen, Fredenborg, Denmark.

Shunatova, N. N., and A. N. Ostrovsky. 2001. Individual autozooidal behaviour and feeding in marine bryozoans. Sarsia 86:113–142.

Shunatova, N. N., and A. N. Ostrovsky. 2002. Group autozooidal behaviour and chimneys in marine bryozoans. Marine Biology 140:503–518.

Silén, L., and J. G. Harmelin. 1974. Observations on living Diastoporidae (Bryozoa Cyclostomata), with special regard to polymorphism. Acta Zoologica 55:81–96.

Smith, A. M., P. D. Taylor, A. Waeschenbach, L. H. Liow, J. S. Porter, A. Ostrovsky, and H. Jenkins. 2017. Cyclostome bryozoans: research strategy and call for action. International Bryozoology Association Bulletin 13:16–18.

Strathmann, R. R. 1973. Function of lateral cilia in suspension feeding of lophophorates (Brachiopoda, Phoronida, Ectoprocta). Marine Biology 23:129–136.

Tamberg, Y., and N. Shunatova. 2017. Tentacle structure in freshwater bryozoans. Journal of Morphology 278:718–733.

Taylor, P. D. 1981. Functional morphology and evolutionary significance of differing modes of tentacle eversion in marine bryozoans. Pp. 235–247 *in* G. P. Larwood and C. Nielsen, eds. Recent and fossil Bryozoa. Olsen & Olsen, Fredenborg, Denmark.

Tenison-Woods, J. E. 1880. Palaeontology of New Zealand: corals and Bryozoa of the Neozoic period in New Zealand. NZ Geological Survey, Didsbury, Wellington.

Thorpe, J. P., D. R. K. Clarke, and M. A. Best. 1985. Natural variation in tentacle number in marine bryozoans and the possible effects of intraspecific and interspecific competition for food. Pp. 319–327 *in* C. Nielsen and G. P. Larwood, eds. Bryozoa: Ordovician to Recent. Olsen & Olsen, Fredenborg, Denmark.

Von Dassow, M. 2006. Function-dependent development in a colonial animal. Biological Bulletin 211:76–82.

Winston, J. E. 1977. Feeding in marine bryozoans. Pp. 233–271 *in* R. M. Woollacott and R. L. Zimmer, eds. Biology of Bryozoans. Academic Press, London.

Winston, J. E. 1978. Polypide morphology and feeding behaviour in marine ectoprocts. Bulletin of Marine Science 28:1–31.

Winston, J. E. 1979. Current-related morphology and behaviour in some Pacific coast bryozoans. Pp. 247–268 *in* G. P. Larwood and M. B. Abbott, eds. Advances in bryozoology. Systematics Association Special Volume No. 13. Academic Press, London.

Winston, J. E. 1981. Feeding behaviour of modern bryozoans. *In* T. W. Broadhead, ed. Lophophorates: notes for a short course. University of Tennessee Studies in Geology 5:1–21.