# Astogenetic morphological variation in the bryozoan *Prophyllodictya gracilis* from the Middle Ordovician of Russia and inferred colony-wide feeding currents

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**Abstract:** The discovery of a relatively large and complete ptilodictyid bryozoan colony enabled morphometric analysis of astogenetic change from the colony base to the periphery. This enabled us to test the hypothesis that the relative area of feeding and non-feeding zooids must be relatively constant across astogenetic growth in this colony. The colony is a stenolaemate cryptostome belonging to the cribrate species *Prophyllodictya gracilis* (Eichwald). It was recovered from the Volkhov Formation (Dapingian Stage of the Middle Ordovician) from the Putilovo Quarry east of St Petersburg, Russia. The colony was digitally imaged so lacuna and branch dimensions could be measured relative to the colony base

BRYOZOAN colonies often readily detach, disarticulate, and fragment before burial (Taylor & James 2013). Diagenetic breakage can also occur after burial due to overburden pressure (Key *et al.* 2016). As a result, large and relatively complete colonies of fossil bryozoans are rare (Cuffey & Fine 2005, 2006; Key *et al.* 2016). When preserved, they enable robust morphometric analysis for testing a variety of hypotheses such as those dealing with palaeoenvironmental change (Hageman *et al.* 2011), growth rates (Reid 2014) or functional morphology (Waugh & Erickson 2002; Key *et al.* 2011).

Relatively large and complete colonies enable the quantification of spatial relationships of skeletal features through colony astogeny. For example, Wyse Jackson & Key (2019) documented the spatial distribution of epizoans and endoskeletozoans across reassembled ramose stenolaemate bryozoan zoaria from the Ordovician of Ohio, USA. Key *et al.* (2016) used the same reassembled colonies to relate branching pattern to colony height. Hageman *et al.* (2011) attributed zooecial spacing across a 20cm-tall cryptostome stenolaemate colony from the Mississippian of Ireland to daily to decadal environmental and colony edge. Branch thickness and width decreased from the colony base to the top of the colony. Lacuna area and the number of autozooecial rows per branch also decreased distally while the number of lacunae per area increased. As a result, there was an astogenetically stable ratio of autozooidbearing skeletal branch area to the total lacuna area across the colony. This characteristic is interpreted as a requirement of colony-wide feeding currents in this cribrate cryptostome colony.

**Key words:** *Prophyllodictya gracilis*, feeding currents, cryptostome, bryozoan, Middle Ordovician, Russia.

change. Of relevance to this study is how relatively large complete colonies can be used to infer convergent evolution in cribrate colony form and feeding patterns between Ordovician, Jurassic and living bryozoans (Taylor 2012). The goal of this project is to understand how a relatively large and complete cribrate cryptostome stenolaemate bryozoan from the Middle Ordovician of Russia managed its colony-wide feeding currents during its growth. We hypothesize that the relative area of feeding and nonfeeding zooids must be relatively constant across astogenetic colony growth in this colony.

## **GEOLOGICAL SETTING**

The colony came from the trilobite-bearing carbonate horizon of the Volkhov Formation exposed in the Putilovo Quarry, *c*. 60 km east of St Petersburg, Russia at 59.8553°N, 31.3975°E (Fig. 1). The 6 m of the Volkhov Formation exposed in the quarry was deposited during the Volkhov Stage, a regional stage of the East Baltic Ordovician succession (Tolmacheva *et al.* 2003, fig. 2;



FIG. 1. Map showing the location of the Putilovo Quarry where the bryozoan colony in this study was found.

Dronov *et al.* 2011, fig. 2; Koromyslova 2011, fig. 1; Dronov 2017, fig. 14). The Volkhov Stage is equivalent to the International Dapingian Stage of the Middle Ordovician, *c.* 470 Ma (Goldman *et al.* 2020, fig. 20.12).

The Putilovo Quarry has yielded a diverse Ordovician bryozoan fauna. Taylor & Rozhnov (1996) reported the cyclostome Goryunovia Koromyslova, 2011, the trepostome Lynnopora lunata Gorjunova & Koromyslova, 2008 and the esthonoporids Esthonopora clara Koromyslova, 2011 and Esthonoporella miranda Koromyslova, 2011. Ernst (2022) reported on the esthonoporids Dianulites collucatus Pushkin, 2002, and the trepostomes Revalotrypa gibbosa (Bassler, 1911), Dittopora sokolovi Modzalevskaya, 1953 and Dittopora annulata (Eichwald, 1860). In addition, two other species of the cryptostome Prophyllodictya Gorjunova in Gorjunova & Lavrentjeva, 1987 other than P. gracilis (Eichwald, 1840) reported herein have also been described from the location: P. intermedia Gorjunova in Gorjunova & Lavrentjeva, 1987 (Ernst 2022) and Prophyllodictya putilovensis Lavrentjeva in Gorjunova & Lavrentjeva, 1993 (Gorjunova & Lavrentjeva 1993).

### MATERIAL AND METHOD

Compared with other bryozoans described from the Baltic basin (Bassler 1911; Koromyslova 2011; Ernst 2022), this 104-mm-long by 111-mm-wide colony of *Prophyllodictya gracilis* (Eichwald, 1840) is relatively large and complete (Fig. 2). The proximal lower quarter of the colony is complete given that the edges of the colony are unbroken. In the distal upper three-quarters of the colony, all of the edges are broken. How much is broken off is indeterminable.

The colony grew from a flat elliptical base that measures 26.07 mm long by 15.07 mm wide. The hard substrate to which it was cemented was flat, and the colony was basically an erect fan. In Stach's (1936) classic classification, this zoarial growth habit would be described as a reteporiform. In Smith's (1995) scheme, this colony is erect rigid fenestrate (ERfe). According to Hageman *et al.*'s (1997) original classification, it is a cemented erect bilaminar branched (CEbb) colony. Based on Hageman *et al.*'s (1998) analytical classification, it would be an erect, cemented, rigid contiguous, oligoserial, bilaminate, no secondary skeletal thickening, sheet, flat, very frequent bifurcations in one plane (fan) made of fused structural units.

Ulrich (1893, p. 179) introduced the term 'cribrose' for this colony form when he described several species from the Ordovician of Minnesota. Bassler (1911) also used cribrose in his monograph on Ordovician taxa from the Baltic region. The most recent review of bryozoans with such rare morphology is that of Taylor (2012), who described this colony form as cribrate, which he defined as a planar colony made of flattened bifoliate fronds that divide and anastomose to enclose oval holes (lacunae). Superficially, cribrate colonies resemble the more common bryozoan colony form called fenestrate. Functionally, however, a critical difference is that cribrate colonies have feeding zooids on both sides of the flattened colonies, whereas they are only on one side in fenestrate colonies (Suárez Andrés & Wyse Jackson 2015, fig. 1). Fenestrules in unilaminate fenestrate colonies allow water to pass through them and waste is vented out through the reverse barren surface. This process is not possible in bifoliate colonies, hence Taylor's (2012) introduction of the term 'cribrate'.

The colony is relatively undeformed. There are a few cracks, but they are barely visible with no visible offset. This preservation suggests that the colony was minimally deformed during fossilization, which is the norm in the Baltic basin famous for its often unlithified sediments,



**FIG. 2.** The ptilodictyid cryptostome stenolaemate bryozoan *Prophyllodictya gracilis* colony used in this study (TCD.60425). It was found in the Putilovo Quarry near St Petersburg, Russia, in the Volkhov Formation from the Volkhov Stage of the Middle Ordovician. Scale bar represents 5 mm.

undeformed bedding and shallow burial. The Ordovician strata lie almost flat with a regional southward dip of  $2.5^{\circ}-3.5^{\circ}$  (Männil 1990). No subsequent orogenies occurred after deposition, and the sample came from the stable southern portion of the Baltic shield, therefore maintaining its undeformed bedding (Ainsaar *et al.* 1999). Burial of these Ordovician sediments did not exceed 2 km in depth (Ainsaar *et al.* 2004). The conodont colour alteration index of these rocks indicates that the Ordovician rocks reached a maximum burial temperature of 80°C (Bergström 1980). Even the older Cambrian sediments experienced only low-temperature diagenetic alteration of clay minerals (Kirsimäe *et al.* 1999). We attribute the general excellent preservation of the colony to shallow burial and post-depositional tectonic quiescence.

The colony is preserved on a bedding plane of a handsized sample of limestone 140 mm long by 122 mm wide by 51 mm thick. Based on Dunham's (1962) standard hand sample-based carbonate classification system, the limestone is a wackestone. To ensure that none of the edges of the colony was obscured by matrix, the matrix around the edges was removed with a Dremel tool until skeleton was reached. Only a few millimetres more of the colony was uncovered by this preparation. An overlapping series of 37 images of the colony were captured using a Dino-Lite Premier digital microscope. These images were stitched together using the automated Photomerge feature in Adobe Photoshop 2020. This montage was manually spot checked for accuracy. Morphometric data were measured on the digital montages with ImagingSource's IC Measure software v2.0.0.286 to the nearest 0.01 mm. Repeatability experiments showed a measurement error of <2.2%.

Branch thickness (BT) was measured with digital callipers to the nearest 0.01 mm. Measurements were taken around the perimeter of the colony where the bifoliate colony edge was fully visible from the exposed surface to the opposite embedded surface.

The following characters were measured for each complete lacuna visible on the colony surface (Fig. 3). Lacunae are openings in the colony created by the coalescing undulating branches. Maximum lacuna length (LL) was measured from the curved proximal margin of the lacuna to the distal apex. Maximum lacuna width (LW) was measured perpendicular to LL. Lacuna area (LA) was measured by outlining each lacuna where it met the branch skeletal walls. Lacuna distance from colony base (LDB) was measured radially from the intersecting point of LL and LW to the centre of the colony base. Lacuna distance from colony edge (LDE) was measured from the



**FIG. 3.** Morphometric characters measured in this study: lacuna length (LL), lacuna width (LW), lacuna area (LA), lacuna distance from colony base (LDB), lacuna distance from colony edge (LDE), branch width (BW), and the number of rows of autozooecia counted along the branch (AC). Scale bar represents 10 mm.

intersecting point of LL and LW to the colony edge defined by the closest of the two thick proximal lateral branches. Branch width (BW) was measured from a lacuna's distal apex to the lowermost point on the curved proximal margin of the closest adjacent lacuna. The number of rows of autozooecia counted (AC) was counted along this straight line across the branch.

The colony is basically planar, but there is some slight (i.e. <3 mm) surface topography on the colony surface. This variation is either from the growth of the colony itself or from distortion during fossilization and represents a <2.7% error across the colony width of 111 mm. All imaging and measurements ignore this variation and assume that the colony surface is planar.

## RESULTS

We were able to take 17 branch thickness measurements around the perimeter of the colony. Branch thickness

decreases from the colony base at 15.07 mm to the top of the colony at 0.82 mm (mean  $\pm$  SD, 3.20  $\pm$  3.32 mm). A total of 454 branch widths were measured. Branches ranged in width from 0.91 to 6.23 mm (mean, 4.16  $\pm$  0.94 mm). The number of autozooecial rows was counted on each of these branches. They ranged from one to 10 (mean, 6.2  $\pm$  1.6).

There were 132 complete lacunae preserved. They ranged in length from 0.93 to 6.98 mm (mean,  $3.73 \pm 1.11$  mm). Lacuna width ranged from 0.54 to 4.38 mm (mean,  $2.01 \pm 0.66$  mm). Lacuna area ranged from 0.26 to  $18.19 \text{ mm}^2$  (mean,  $5.40 \pm 3.04 \text{ mm}^2$ ). Using lacuna length/width as a proxy for shape, the lachrymiform lacunae are on average twice as long as wide (mean,  $1.92 \pm 0.48$ ; range, 0.95–4.25). The 39 lacunae closest to the left and right proximal edges of the colony ranged from 5.93 to 33.51 mm to the edge (mean,  $19.19 \pm 8.14$  mm).

Institutional abbreviation. TCD, Geological Museum, Trinity College Dublin, Ireland.

# SYSTEMATIC PALAEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831 Class STENOLAEMATA Borg, 1926 Superorder PALAEOSTOMATA Ma *et al.*, 2014 Order CRYPTOSTOMATA Vine, 1884 Suborder PTILODICTYINA Astrova & Morozova, 1956 Family PTILODICTYIDAE Zittel, 1880 Subfamily RHINIDICTYINAE Ulrich, 1893 Genus PROPHYLLODICTYA Gorjunova *in* Gorjunova & Lavrentjeva, 1987

*Type species. Prophyllodictya intermedia* Gorjunova *in* Gorjunova & Lavrentjeva, 1987 from the Middle Ordovician (Floian Stage, Volkhov horizon) of Maardu, Estonia and the St Petersburg area, Russia.

*Diagnosis.* Colonies erect, lenticular, frondose or reticulate; branches oval or lens-shaped in transversal section; mesotheca straight, without hyaline rods; autozooecia long, tubular, bending in exozone; diaphragms rare or absent; hemisepta absent; autozooecial apertures oval, arranged in alternating rows on the colony surface; low ridges between apertures bearing paurostyles present; exozonal tubes present; maculae lacking autozooecia and bearing paurostyles and exozonal tubes occurring (from Ernst 2022, p. 60).

## Prophyllodictya gracilis (Eichwald, 1840) Figures 1, 3

1840 Eschara gracilis Eichwald, p. 205.

1842 Gorgonia gracilis (Eichwald); Eichwald, p. 43, fig. 1(4).

- 1855 Thamniscus gracilis (Eichwald); Eichwald, p. 454.
- 1860 Micropora gracilis (Eichwald); Eichwald, p. 393, pl. 33, fig. 4a, b.
- 1911 Stictoporella gracilis (Eichwald); Bassler, p. 130, figs 54, 55, pl. 7, figs 1–3.
- 1985 *Stictoporellina gracilis* (Eichwald); Taylor & Curry, p. 156.
- 1987 Prophyllodictya gracilis (Eichwald); Gorjunova in Gorjunova & Lavrentjeva, p. 55.
- 1993 Prophyllodictya gracilis (Eichwald); Gorjunova & Lavrentjeva, p. 37.
- 2011 Prophyllodictya gracilis (Eichwald); Koromyslova, p. 947.

*Material.* One specimen from the Putilovo Quarry, 60 km east of St Petersburg, Russia; Middle Ordovician (Dapingian Stage, Volkhov Formation). Specimen and two acetate peels made from it deposited in the Geological Museum, Trinity College Dublin; accession number TCD.60425.

External description. Colony erect, arising from a robust base that splits into two strongly skeletal proximal branches from which develop a cribrate zoarium. The basal branch and proximal thickened branches are striated and composed of kenozooecia (= cenozooecia of Gorjunova & Lavrentjeva 1987, p. 51) in elongate arrays with small circular apertures. Extrazooecial skeleton lacking. Zoarium composed of bilaminate flattened branches that are undulate and coalesce to produce lachrymiform lacunae. Kenozooecia line the innermost portions of lacunae and the pointed area of the coalescent distal branch for a short distance. Distal margins of lacunae usually semicircular except where some coalescing branches terminate and indent the margin. Branches with an average of six rows of autozooecia separated by a low ridge or rib on which short paurostyles are arranged in single rows. Autozooecia apertures circular to subcircular in shape. Exilazooecia with small circular openings located proximally of autozooecial apertures. Maculae absent.

*Internal description.* Mesotheca thin, generally straight with autozooecia budded from either side. Autozooecia diaphragms absent. Chambers thin-walled in endozone, thickened in exozone with exilazooecia at a high angle to the zoaria surface. Paurostyles developed within exozone.

*Remarks.* Herein both terms 'exilazooecia' and 'kenozooecia' are used for polymorphs that are seemingly identical in structure but are situated in different parts of the colony. In some trepostome taxa, the former could be referred to as 'exozonal tubes' (Ernst 2022). The term 'kenozooecia' is usually restricted to polymorphs in modern cheilostomes and cyclostomes that are developed in stereom that lack autozooecia and which fulfil a strengthening purpose among others (Taylor 2020, p. 72). The crowded polymorphic zooids situated in the basal attachment and stem and two thickened proximal lateral branches, and in lacunae, as developed in *Prophyllodictya gracilis*, bear a close resemblance to kenozooids and are probably structural in function whereas the small circular openings between the autozooecia, referred to herein as exilazooecia, occur either singly or in small clumps, and it is more likely that they are space fillers in the exozone.

Prophyllodictya gracilis resembles in its cribrate form the cribrate colonies of *P. intermedia* Gorjunova *in* Gorjunova & Lavrentjeva, 1987 but it differs from those colonies of *P. intermedia* that develop ramose and foliate zoarial forms. It differs from *P. flabellaris* (Bassler, 1911), which is foliate in form and *P. lauta* Lavrentjeva *in* Gorjunova & Lavrentjeva, 1987 and *P. putilovensis* Lavrentjeva *in* Gorjunova & Lavrentjeva, 1993, both of which form ramose colonies.

## DISCUSSION

#### Branch thickness

As with many erect branching organisms, structural thickness increases proximally in a logarithmic fashion to enhance functional rigidity (Ball 2016). In our colony the branch thickness decreases distally in a logarithmic fashion (Distance =  $-38.25\ln(\text{thickness}) + 94.013$ ;  $R^2$  = 0.8953) (Fig. 4). In erect branching bryozoans, this feature manifests as a wide basal attachment followed by distal thinning. Basal attachments showing distal thinning of colonies during early astogeny are rarely preserved (McKinney & King 1984; Gorjunova & Lavrentjeva 1987; Taylor 2020). In those cases in which the basal attachment is preserved, the narrowing is ubiquitous (Gorjunova & Lavrentjeva 1987, fig. 1; Hageman et al. 1998, fig. 6.1; Taylor & Gordon 2003, fig. 7.D; Taylor 2020, fig. 4.12). So much so, that wide basal attachments have become incorporated into our stylized zoarial habits of cemented erect colonies (Hageman et al. 1998, figs 3.1, 3.2; Taylor & James 2013, fig. 7D, F, G, H, I; Taylor 2020, fig. 2.2). This basal morphology is also true for cemented erect bilaminate colonies of relevance to this study (Hageman et al. 1998, fig. 3.5).

This early astogenetic thickening proximally of the colony was already established by the Early Ordovician (Gorjunova & Lavrentjeva 1987; Dzik 1992; Ma et al. 2015). The basal thickening often involves extrazooecial secondary calcification (Tavener-Smith 1974, p. 161, 163; McKinney & King 1984, p. 863; Gorjunova & Lavrentjeva 1987, p. 51; Taylor 2020, p. 89) and can be seen in a variety of bryozoans from fenestellids (e.g. Parachasmatopora(?) sp. in Dzik 1992, fig. 8B) to cheilostomes (e.g. Metrarabdotos moniliferum in Taylor 2020, fig. 4.12). The colony-wide distal thinning in branch width seen in this colony (Fig. 4) is evident in cyclostomes (e.g. Terebellaria ramosissima in Taylor 2020, fig. 4.10) and other ptilodictyid cryptostomes (e.g. Prophyllodictya intermedia in Ernst 2022, fig. 16F). Using Ernst's (2022, fig. 16F) longitudinal thin section of P. intermedia, we measured branch thickness distally from the base of the colony to the top. It too exhibited decreasing branch thickness distally in a logarithmic fashion (Distance = -3.159ln(thickness) + 2.533; R<sup>2</sup> = 0.9197).



FIG. 4. Plot showing branch thickness decreasing exponentially in a distal direction from colony base. Error bars indicate a maximum 2.2% measurement error.

In the fenestrate genera Lyropora and Lyroporella, thickening through extrazooecial calcification of the proximal lateral margins of colonies occurs, and from these a delicate meshwork of branches connected by dissepiments grows distally (McKinney & Wyse Jackson 2015, p. 29). However, unlike in Prophyllodictya, which has an erect habit, in these lyre-shaped fenestrate taxa the thickened margins rest on the substrate and act to stabilize, by virtue of their weight, the colony, which remains uncemented. The meshwork grows parallel and just above the substrate surface (McKinney 1994). Whereas the thickened lateral margins undoubtedly had a structural function that weighed down the colony, they may also have provided a strong basal margin that protected the delicate meshwork that grew distally from it from breakage by any turbulent water currents. In the same way, the strong robust proximal lateral branches in Prophyllodictya allowed for the development of more delicate coalescing branches above them and protected them from fragmentation in strong current flow that could have acted on the erect colony.

Therefore, the vertical growth of the colony with its thinner branches distally (Fig. 4) would have become limited due to breakage from ambient water currents. During the Volkhovian age, the palaeoenvironments around the St Petersburg area were dominated by shallow-water, storm-dominated bioclastic wackestone deposition (Knaust *et al.* 2012). The thin distal edges of larger colonies would have been susceptible to breakage during these storms. Ambient water currents also had a disruptive effect on the self-generated water circulation patterns in the cribrate bryozoans discussed below (Taylor 2012). Schmidt & Bone (2004) reported that this colony form was prevalent in Cainozoic high-energy environments such as those during the Volkhovian age.

#### Branch width

Mean branch width in this species (4.16 mm) was slightly more than the congeneric species Prophyllodictya intermedia Gorjunova in Gorjunova & Lavrentjeva, 1987 at 3.3-3.8 mm (Ernst 2022). Branch width in our colony significantly decreases distally with increasing radial distance from the colony base (Fig. 5). Branch width did not significantly change relative to distance from the colony edges (linear regression,  $R^2 = 0.0262$ , p > 0.05). This feature suggests that management of previously filtered water at the colony surfaces (sensu Taylor 2012, fig. 6a) is being handled by changes in branch width, which is directly related to lacuna size as indicated below. We interpret this morphological relationship to mean that lacunabased exhalent chimneys are playing a bigger role in moving previously filtered water away from the colony surface than the colony edges.

#### Number of autozooecia per branch

The mean number of autozooecial rows per branch (seven) was less than that in the congeneric species *P. intermedia* at 8–10 (Ernst 2022). As expected, due to



FIG. 5. Plot showing branch width decreasing in a distal direction from colony base. Error bars indicate a maximum 2.2% measurement error.

simple space constraints, the wider the branch, the more autozooecial rows it can hold. Mean branch width was significantly correlated with the number of autozooecial rows ( $R^2 = 0.4831$ ;  $p \le 0.0001$ ). More autozooecia on a branch means more feeding currents coming into the colony surface (McKinney 1986; Taylor 2012). More incoming feeding currents means greater need for excurrent chimneys or being closer to a colony edge (Dassow 2005; Key *et al.* 2011).

The number of autozooecial rows per branch significantly decreases distally with increasing distance from the colony base (Fig. 6). The number of autozooecial rows per branch did not significantly change relative to distance from the colony edges (linear regression,  $R^2 =$ 0.0970, p > 0.05).

### Lacuna length, width and area

Mean lacuna length in this colony (4.26 mm) was longer than that in the congeneric species *P. intermedia* at 2.7– 3.6 mm (Ernst 2022). Mean lacuna width in this species (2.32 mm) was similar to that in *P. intermedia* at 2.3– 2.5 mm (Ernst 2022). Lacuna length and width in our colony significantly decreases distally with increasing distance from the colony base (Figs 7, 8). Lacuna length significantly decreases with increasing distance from the colony edges (linear regression,  $R^2 = 0.2742$ ,  $p \le 0.001$ ), but lacuna width did not (linear regression,  $R^2 = 0.0749$ , p > 0.05). Lacuna area significantly decreases distally with increasing distance from the colony base (Fig. 9) as well as with increasing distance from the colony edges (linear regression,  $R^2 = 0.2276$ ,  $p \le 0.01$ ).

Why are the  $R^2$  values so low in these correlations? There are two sources of variation in the morphometric characters measured here. First, distance from colony base combines information from two different characters: distance above substrate and distance from colony edge. Distance above the substrate would be measured perpendicular to the substrate up into the water column. Distance from the colony base was measured slightly oblique to this, as radially from the colony base. Second, modular organisms such as bryozoans are more variable in their morphology than solitary organisms (Di Martino & Liow 2022).

# Feeding currents and self-generated water circulation patterns

In some stenolaemate bryozoans there is evidence that feeding zooids were active only in distal and younger portions of the colonies and that the older colony areas had undergone senescence and had ceased to support active feeding polypides. In trepostomes for which there is most evidence, this is indicated by the occurrence of brown bodies, which are the degraded remains of dead polypides (Morrison & Anstey 1979; Boardman 1999; Key *et al.* 2008), the capping of autozooecial chambers by terminal diaphragms that closed them off for active occupation (Boardman 1999, 2001), or calcitic infilling of the chambers *in vivo*. Within cryptostomes, this evidence is



**FIG. 6.** Plot showing number of autozooecial rows per branch decreasing in a distal direction from colony base. Error bars indicate a maximum 2.2% measurement error.



FIG. 7. Plot showing lacuna length decreasing in a distal direction from colony base. Error bars indicate a maximum 2.2% measurement error.

less common. In at least one rhabdomesine cryptostome, terminal diaphragms are known (Blake 1983, p. 537) and they have also been reported in the Ordovician ptilodic-tyoid *Trigonodictya* cf. *T. acuta* (Hall, 1847) (Kar-klins 1983) but their development in cryptostomes is not widespread. Brown bodies have not been reported in cryptostomes. In this specimen of *P. gracilis* we have not observed terminal diaphragms or calcite chamber infills and have not been able to document the presence of

brown bodies. It is therefore entirely feasible that the whole of the colony would have been actively feeding simultaneously. This would create the need for colonywide feeding currents.

Gorjunova (2009, fig. 8) illustrated a model of water flow dynamics in anastomosing bifoliate (more precisely, cribrate) colonies in which water flow took place through the fenestrules (more precisely, lacunae) from either direction. One assumes that this bi-directional



FIG. 8. Plot showing lacuna width decreasing in a distal direction from colony base. Error bars indicate a maximum 2.2% measurement error.



FIG. 9. Plot showing lacuna area decreasing in a distal direction from colony base. Error bars indicate a maximum 2.2% measurement error.

antagonistic flow did not occur at the same time, because to do so would be chaotic and disruptive to efficient feeding and waste dispersal. This earlier interpretation is counter to Taylor's (2012) model adopted herein of water flow in which two sets of incurrents and excurrents are independent of each other, confined to opposite surfaces of the bifoliate colony, and do not interact across the mesothecal or mid-colony branch line. The incurrents are located over the autozooecia-bearing branches, whereas the excurrents are located over the lacunae (Taylor 2012, fig. 6a).

What is the function of the kenozooecia and do they contribute to the functioning of the lacunae in water circulation? On branches, autozooecia are on average developed in six rows but become replaced by kenozooecia closer to the lacunae (Fig. 3). These kenozooecia are arrayed in several rows on either side of the mesotheca that is the central line of the flattened branches from when autozooecia are budded back to back. There is no evidence that they ever contained polypides such as nanozooecia or secondary nanozooecia as seen in some modern and fenestrate bryozoans, respectively (Bancroft 1986). If they had, then they may have enabled increased exhalent generation through the beating of single tentacles. However, without polypides, the kenozooecia simply act as space fillers. Space filling problems in stenolaemate bryozoans have been shown to be solved by deploying similar types of heterozooecia (e.g. mesozooecia in the Permian *Tabulipora*; Key *et al.* 2001).

Taylor (2012, p. 209) noted that the kenozooecia serve an additional purpose to space filling. Their positioning along the margins of a lacuna increases the lacuna's area for the discharge of exhalent water flow centred over the lacunae. The lophophores of the autozooecia generated an incurrent above the branch that brought in food particles, which would have been ingested (Dassow 2005). Depleted water and any waste materials would have then been passed laterally over the branch surface sloping towards the lacuna. There, this depleted water would have ponded back to back against a similar water body generated on the opposite side of the branch, and the residual energy of the incurrents on either side would have forced the excurrents to move upwards over lacunae in opposite directions from the sides of branches. In P. gracilis, monticules or maculae that would have acted as centres for exhalent currents, are not developed, and without them the lacunae functioned in the same way.

Why do the branch widths and their corresponding number of rows of autozooecia, as well as in the lacuna area, all decrease distally? The fan-like shape of the colony is geometrically similar to the sector of a circle (imagine a pizza slice). The area of the sector of a circle increases proportionally with the radius (r) squared. As the colony grew in area (i.e. proportional to  $r^2$ ), the number of feeding autozooids creating incurrents would have increased exponentially. To balance this, more excurrent chimney area needed to be developed. This increase in area could be achieved through more and/or larger lacunae. But, as discussed above, the lacunae actually decrease in size distally (Fig. 9). Therefore, the number of lacunae had to increase. This feature can be seen below in the unchanging relative proportion of the skeletal branch area relative to the total lacuna area across the colony.

The exposed surface area of the colony excluding incomplete lacunae is 7167 mm<sup>2</sup>. The combined surface area of the 132 complete lacunae is 712 mm<sup>2</sup>. Thus, the proportional area of lacunae is 10%. This value falls within the range of 7–24% reported by Taylor (2012, fig. 5) for cribrate cryptostome colonies. There was no significant difference in this proportion between the proximal half of the colony (11%) and the distal half (10%). As the colony grew, the first branches and lacunae that formed

above the colony base expanded over time, hence the proximal branches and lacunae are larger than the distal ones, but the relative proportion of skeletal area (i.e. incurrent generating autozooecia) and excurrent area (i.e. lacunae) remained constant at *c*. 10%. The more distal thinner branches and smaller lacunae would have become bigger if the colony had continued to grow, but the 10% proportion would have remained constant. As expected, excurrent area, as defined by lacuna area, is positively and significantly correlated with incurrent area, as defined by the number of autozooecial rows per branch (linear regression,  $R^2 = 0.0764$ ,  $p \le 0.01$ ).

## CONCLUSION

*Prophyllodictya gracilis* appears somewhat unusual in cribrate bryozoans in that branch width and lacunae area decrease progressively distally through the colony. Although others have not collected data to quantitatively analyse this, it appears that in most cribrate colonies, branch width and lacuna area appear to remain stable as the colony grows. This astogenetic stability is qualitatively seen in the Recent cheilostome *Adeona albida* Kirchenpauer, 1880 (Taylor 2012, fig. 3a), the Devonian cryptostome *Clathropora intertexta* Nicholson, 1874 (Taylor 2012, fig. 3e), and the Ordovician cryptostome *Stictoporellina* sp. (Taylor 2012, fig. 3f). This stability may simply be an artefact of low R<sup>2</sup> values in our species and lack of similar morphometric analyses in the other species.

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## DATA ARCHIVING STATEMENT

The supporting data have been archived at Trinity's Access to Research Archive (TARA): https://doi.org/10. 25546/101924

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