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HOW TO BUILD A RAMOSE TREPOSTOME

Marcus M. KEY, Jr.
Department of Geology, Dickinson College,
CARLISLE, PA 17013-2896 (U.S.A.)

ABSTRACT. – As a ramose trepostome grows, the colony faces many constructional problems. These include filling the space between autozooids at the colony surface, branch strength, and density of feeding zooids at the colony surface. To determine how these problems are solved, eight quantitative morphologic characters relating to these constructional problems were measured. 176 colonies from 10 Ordovician trepostome species were analyzed. Correlation coefficients between these characters reveal that solutions to these three problems are often interrelated. Solutions to one problem may improve or worsen other problems. Some solutions were found to occur in specific combinations with other strongly correlated characters. The repeated occurrence of these morphotypes in unrelated lineages indicates trepostome morphogenesis may be constrained to some degree by these constructional needs.

KEY-WORDS. – Bryozoa, ramose trepostome, constructional, morphogenesis, Ordovician.

RÉSUMÉ. – Quand un Trépostome rameux se développe, la colonie se trouve face à de nombreux problèmes de construction. Ceux-ci comprennent le remplissage de l'espace entre les autozoïdes à la surface de la colonie, la résistance d'une branche et la densité des zoïdes nourriciers à la surface de la colonie. Pour déterminer la façon dont ces problèmes sont résolus, 8 caractères morphologiques quantitatifs liés à ces questions de construction ont été mesurés. 176 colonies appartenant à 10 espèces ordoviciennes ont été analysées. Les coefficients de corrélation entre ces caractères révèlent que les solutions à ces trois problèmes sont souvent intriquées. Les solutions d'un problème peuvent améliorer les autres problèmes ou leur nuire. Il a été constaté que certaines solutions existent dans des combinaisons spécifiques avec d'autres caractères étroitement corrélés. L'existence répétée de ces morphotypes dans des lignées sans rapport entre elles montre que la morphogénèse des Trépostomes peut subir à un certain degré des contraintes dues à ces impératifs de construction.

MOTS-CLÉS. – Bryozoa, Trépostome rameux, construction, morphogénèse, Ordovicien.

INTRODUCTION

An organism's form is controlled by phylogenetic, functional, and fabricational constraints (SEILACHER, 1970). This study deals with the effects of functional and fabricational constraints (here termed constructional constraints) on function in ramose trepostomes. When analyzing the constructional constraints on an organism it is important to treat the organism as an integrated entity, not as a collection of independent characters (GOULD & LEWONTIN, 1979). To do so would ignore the fact that an organism's characters exist within the constraints imposed by other characters. For example, in a trepostome one can not consider the exozone independently of the endozone, because the size of the endozone dictates the initial size of the exozone. GOULD and LEWONTIN (1979) also warn of falling into the trap of constructing untestable adaptationist stories. To avoid this, a biomechanical approach is taken in this study that permits testing with simple physics and geometry.

Due to the colonial nature of bryozoans where zooids must be integrated into a colony, ramose trepostomes face many constructional demands. This paper focuses on three such demands. 1) The colony must fill the space between autozooidal apertures to maintain a confluent growth surface. 2) The colony must be strong enough to withstand breakage. 3) The colony must have enough feeding autozooids at the colony surface to supply sufficient nutrients for the entire colony. The focus of this study is on how these problems are solved and how solutions to one problem affect the other problems.

MATERIALS AND METHODS

To examine solutions to the constructional demands within a colony, 176 colonies belonging to 10 species of ramose trepostomes were chosen from the Ordovician Simpson Group. The Simpson Group was deposited in North America in the Southern Oklahoma Aulacogen Basin during the Chazyan, Blackriveran, and Rocklandian Stages of the Middle Ordovician (ROSS *et al.*, 1982). The colonies were collected from outcrops in the Arbuckle Mountains and Criner Hills of south-central Oklahoma.

The 10 species used in this report represent a single lineage (KEY, 1988). The species include *Champlainopora chazyensis* (ROSS, 1963), *Amplexopora conferta* (CORYELL, 1921), *A. winchelli* ULRICH, 1886, *Hallopora dubia* LOEBLICH, 1942, *H. macrostoma* LOEBLICH, 1942, and *H. pachymura* LOEBLICH, 1942. The other four species are new. Their preliminary taxonomic descriptions are presented by the author elsewhere (KEY, 1988).

Eight quantitative characters were measured on each colony. Measurements were made with a morphometric image analysis system using digitized video images of thin sections and acetate peels. Measurement error was less than 3.8%. Surface angle, autozooid living chamber cross-sectional area in the exozone (aperture area), interaperture distance in the exozone (wall thickness), and number of complete mesozooids per mm^2 in the exozone (mesozooid abundance) were all measured up to 10 times per colony. These data were averaged to obtain colony mean values. Endozone diameter, exozone width, and branch diameter were measured once per colony. These were used to calculate axial ratio. Even though axial ratio is not a completely independent character, it was calculated here because it is traditionally reported and it provides a quick measure of the endozone diameter/branch diameter ratio.

RESULTS

To determine the constructional relationships between the eight characters, a Pearson correlation matrix was calculated from the raw data using pairwise deletion (Table 1). The correlation coefficients between these characters reveal many interesting relationships which provide insight into the solutions to the constructional problems faced by ramose trepostome colonies.

	SURFACE ANGLE	ENDOZONE DIAMETER	EXOZONE WIDTH	BRANCH DIAMETER	AXIAL RATIO	APERTURE AREA	WALL THICKNESS	MESOZOOID ABUNDANCE
SURFACE ANGLE		166	166	166	166	127	166	101
ENDOZONE DIAMETER	0.457		167	167	167	127	167	101
EXOZONE WIDTH	0.651	0.271		167	167	127	167	101
BRANCH DIAMETER	0.667	0.873	0.706		167	127	167	101
AXIAL RATIO	-0.222	0.563	-0.592	0.114*		127	167	101
APERTURE AREA	0.165*	0.474	0.118*	0.409	0.295		135	104
WALL THICKNESS	-0.149*	-0.482	0.004*	-0.353	-0.451	-0.319		105
MESOZOOID ABUNDANCE	-0.147*	-0.080*	-0.316	-0.235	0.246	0.218	-0.289	

Table 1. Pearson correlation matrix calculated from raw data. Correlation coefficients are shown below the diagonal. Frequencies are shown above the diagonal. Asterisks indicate correlation is insignificant at P = 0.05.

Tableau 1. Matrice de corrélation de Pearson calculée d'après les données brutes. Les coefficients de corrélation sont figurés au-dessous de la diagonale, les fréquences au-dessus. Les astérisques indiquent que la corrélation n'est pas significative pour P = 0.05.

DISCUSSION

If a ramose trepostome colony is cut transversely, the exozone looks like the outer part of a bicycle wheel. If one thinks of the spokes on a wheel as being thin tubes, they are analogous to the autozooids in the exozone. As the colony grows, the autozooids become longer and the colony surface area increases. The autozooids do not appreciably increase in diameter through the exozone just, as the spokes on a wheel do not. As colony growth continues, the autozooids become isolated like the spokes on a wheel at the rim versus the hub. As a result, the percent of total colony surface area occupied by the autozooidal apertures decreases, and the area between the autozooids increases. One of the constructional problems facing ramose trepostomes is how do colonies occupy this space. The space between the autozooids must be and is occupied for several reasons. First, if it was not occupied, the autozooids would not be in physical contact and they would easily break. Second, the colony branches would easily break. Finally and most importantly, trepostomes require a confluent outer membrane for budding and nutrient exchange (BORG, 1926; BOARDMAN, 1971).

The simplest solution to this constructional problem would seem to be to reduce the area between autozooids by reducing the colony surface aera. Colony surface aera could be reduced by making a colony with a smaller branch diameter. This may affect the feeding capacity of the colony as well as its strength. This is a good example of how a solution to one problem influences other problems. Colonies with wider branches usually have monticules for efficient colony-wide feeding currents (BANTA *et al.*, 1974; MCKINNEY, 1986) and they usually are less susceptible to breakage (CHEETHAM & THOMSEN, 1981). Colonies with narrow branches may not need colony-wide feeding currents to dispose of previously filtered water (McKINNEY, 1986) and they generally are more susceptible to breakage (CHEETHAM & THOMSEN, 1981). This is not necessarily detrimental in an evolutionary sense because such colonies may be able to more easily utilize asexual colony replication through fragmentation (*sensu* McKINNEY, 1983).

Exozone width

Reducing the exozone width would reduce the colony surface area because it would decrease the branch diamater. If the exozone width is decreased, the colony would be weaker. Reducing exozone width makes a colony weaker for two reasons: colony strenght is proportional to exozone width and branch diameter.

To understand the cause of these relationships requires a review of stresses and cross-sectional shapes. The following discussion is modified from WAINWRIGHT *et al.* (1976). A branch from a ramose trepostome has the general shape of a cylinder. The transverse section of a cylinder (*i.e.* the branch) is an important factor in determining its strength.

Branch strength is proportional to **I/R. I** is the second moment of area and is usually referred to as the moment of inertia of the section. In a circle like that of a transverse section of a ramose trepostome branch, it is a measure of how material is distributed about the axis of the branch. For a circle:

$$\mathbf{I} = \frac{\pi}{4} (\mathbf{R}^4 - \mathbf{r}^4)$$

$$\mathbf{R} = \mathbf{r} + \mathbf{t}$$

In a ramose trepostome, **R** is the radius of the branch, **r** is the radius of the endozone, and **t** is the width of the exozone. This means that branch strength is proportional to endozone diameter, exozone width, and branch diameter. By placing more skeletal material away from the branch axis the branch becomes stronger. This translates to having a wide, ligthtly calcified endozone surrounded by a wide, highly calcified exozone. These relationships have been demonstrated empirically in branching cheilostomes (CHEETHAM & THOMSEN, 1981).

Endozone diameter

Reducing the exozone width may help the problem of how to occupy the area between autozooids, but it will make the colony weaker. The other way to reduce colony surface area is to make a colony with a narrower endozone. There are two effects of decreasing the endozone diameter. First, due to the relationship between branch strength and diameter, decreasing the endozone diameter would decrease the strength of the colony. Second, decreasing the endozone diameter would result in relatively fewer autozooids available to occupy any given surface area. The reason for this is that as the endozone diameter is decreased, the colony's volume decreases relatively more than its surface area. This is because in a ramose colony, each branch is analogous to a cylinder. In a cylinder, volume increases as a power function of the radius while surface area increases linearly:

$$\text{VOLUME OF A CYLINDER} = \mathbf{H} \times \pi \times \mathbf{R}^2$$

$$\text{SURFACE AREA OF A CYLINDER} = \mathbf{H} \times 2 \times \pi \times \mathbf{R}$$

H is the height of the cylinder and **R** is the radius. Because the autozooids are budded in the endozone, the more volume occupied by the endozone the more autozooids available to occupy any given surface area. So a good solution to both the branch strengh and surface area problems is to increase the endozone diameter.

Surface angle

Another solution to the constructional problem of occupying the space between autozooids would be to decrease the surface angle. The surface angle is the angle at which the autozooids intersect the colony surface. With a maximum surface angle of 90°, autozooidal aperture area is minimized. A smaller surface angle would cause each autozooidal aperture to occupy more area at the colony surface. Increasing the surface area that each autozooidal aperture occupies would reduce the number of autozooids per unit area at the colony surface. This could reduce the feeding capacity of the colony because there would be fewer feeding zooids per unit area.

Surface angle is also related to branch strengh because for a colony to have a higher surface angle generally requires a thicker exozone. The relationship between surface angle and exozone width is evidenced by their highly significant, positive correlation (Table 1). A higher surface angle requires a thicker exozone because it takes longer (ontogenetically) for the zooids to grow from their tangential orientation (relative to the colony surface) in the endozone to their more perpendicular orientation in the exozone. Increasing the surface angle not only increases the feeding capacity of the colony, but it also makes for a stronger colony due to the relationship between branch strength and exozone width.

The relationship between branch strength and packing of autozooids at the colony surface can be seen in the Pearson correlation coefficients between surface angle, endozone diameter, exozone width, and branch diameter. These four characters are all significantly, positively correlated (Table 1). Based on these 10 species, colonies with high surface angles tend to have large diameter endozones, thick exozones and large diameter branches. These colonies are theoretically stronger and have more feeding zooids per unit area at the colony surface. Examples of this morphotype include species from several diverse lineages: *Amplexopora conferta* (CORYELL, 1921), *A. septosa* (ULRICH, 1879), *A. winchelli* ULRICH, 1886, *Hallopora macrostoma* LOEBLICH, 1942, *Homotrypa obliqua* ULRICH, 1882, and *Rhombotrypa quadrata* (ROMINGER, 1866). Colonies with low surface angles tend to have small diameter endozones, thin exozones and small diameter branches. These colonies are theoretically more susceptible to breakage and have fewer feeding zooids per unit area at the colony surface. Examples of this morphotype include species from several diverse lineages: *Bythopora herricki* ULRICH, 1886, *Champlainopora chazyensis* (ROSS, 1963), *Eridotrypa aedilis* (EICHWALD, 1855), *E. mutabilis* ULRICH, 1893, and *Hallopora pachymura* LOEBLICH, 1942.

Wall thickness

Another solution to the constructional problem of occupying the space between autozooidal apertures is to develop thick autozooidal walls. These walls fill in the space between autozooidal apertures. In most trepostomes, the autozooidal walls thicken in the exozone. Unfortunately, thicker walls mean smaller autozooidal apertures. This is evidenced in the correlation matrix (Table 1) where aperture area has a highly significant, negative correlation with wall thickness. Smaller autozooidal apertures mean smaller mouths which limit the size of ingestible food particles (WINSTON, 1981).

Mesozooid abundance

Another viable solution to the constructional problem of occupying the space between autozooids is to develop exozonal mesozooids which serve as space fillers between autozooids (BOARDMAN, 1983). The presence of mesozooids in the exozone may be an alternative to having thick autozooidal walls. The Pearson correlation matrix (Table 1) indicates wall thickness has a highly significant, negative correlation with mesozooid abundance. Colonies with abundant mesozooids tend to have thinner autozooidal walls. This may reflect the space filling capacity of mesozooids eliminating the need for thick autozooidal walls.

CONCLUSIONS

There are many constructional problems faced by ramose trepostome colonies during growth. This paper focused on three of these problems: occupying the space between autozooids at the colony surface, branch strength, and packing feeding zooids at the colony surface. These three constructional needs are interrelated. It was shown how the solution to one of these constructional problems has direct implications on solutions to the other problems.

Correlation coefficients revealed the presence of repeated occurrences of colonies with distinct morphologies. Colonies tended to have wide endozones, thick exozones, and high surface angles or narrow endozones, thin exozones, and low surface angles. This suggests that patterns of morphogenesis in ramose trepostomes may fall into discrete morphotypes. This is not to imply that intermediate morphotypes do not occur. They do, for example *Hallopora dubia* LOEBLICH, 1942. But based on this small sample of 10 species of Middle Ordovician ramose trepostomes, intermediate morphotypes are rare.

The existence of these patterns raises other interesting questions. How wide spread are these patterns in other trepostome and non-trepostome lineages? Do species with encrusting or massive growth habits exhibit similar constructional constraints? The repeated occurrences of these specific morphotypes in different lineages may shed some light on the evolutionary processes producing the patterns. This study examined 10 species from a single lineage. As a result it is impossible to distinguish the influence of phylogenetic constraints from convergent or divergent evolution. Expansion of this research program into different lineages will permit the differentiation of phylogenetic constraints (*i.e.* similar patterns restricted to sister clades) from convergent evolution (*i.e.* similar patterns in phylogenetically unrelated clades).

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