Ontogenetic and Systematic Study of *Eucystis* (Diploporita: Echinodermata)

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Introduction

Blastozoan echinoderms are not well understood in terms of their ontogeny and paleoecology. Diploporitan echinoderms, blastozoans with double pore (diplopore) respiratory structures (Sprinkle, 1973), are especially poorly understood based on typical poor preservation of morphologically distinct areas and a significant lack of juvenile specimens, so understanding ontogenetic changes from juvenile to adult stages is difficult. *Eucystis*, a diploritan echinoderm, has the longest temporal range (Ordovician-Devonian) and one of the widest geographical ranges of diploporitan echinoderms, with fossil collections from Laurentia, Gondwana, and Baltica. They are identifiable by comparatively long, multibranching ambulacra that end in varying numbers of brachiole facets, ovate to spherical theca, pentagonal thecal plates and a holdfast attachment structure of varying size and shape (Fig. 1; Kesling, 1967).

An unusually well-preserved collection of *Eucystis angelini*, collected from the Upper Ordovician Boda Limestone of Sweden and reposited at the Geological Institute of Tallinn (GIT), preserves a wide range of ontogenetic stages and includes rare juvenile examples. The juveniles allow for better understanding of growth patterns of *Eucystis*. This study will further the understanding diploporitan growth patterns, which then can be compared with other early Paleozoic echinoderm ontogenies and will allow for better understanding in diploporitan paleoecology. This study highlights the importance of finding juvenile fossils, and how critical they are in assessing ontogenetic growth of echinoderms.

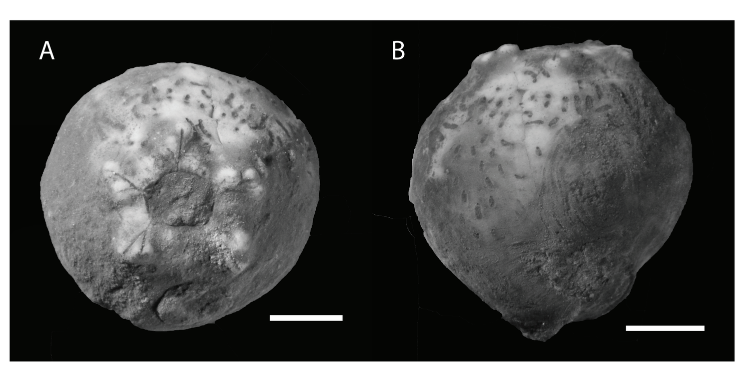

Fig. 1. GIT 639-84. *Eucystis* is characterized by multibranching ambulacra that end in varying numbers of brachiole facets (A) and an ovate to spherical theca with pentagonal thecal plates.

Materials and Methods

A morphometric study of *Eucystis angelini* was performed on a large collection of specimens (22) from the Upper Ordovician Boda Limestone. Measurements of the body (theca), peristome (mouth), periproct (anus), feeding ambulacra, plates, respiratory structures, and the holdfast were taken and analyzed to quantify this species' growth patterns. Each measurement was repeated five times to ensure precision and accuracy with a pair of digital callipers. The data was then recorded by hand and then transferred to a database file. For measurements such as ambulacra length, number of bracioles per ambulacra and length of brachioles, an average was taken

Each measurement (e.g., width of theca, width of peristome) was divided by the corresponding thecal height for each specimen in order to remove size bias from the dataset. Normalized measurements were plotted against each other in scatter plots. Trend lines were added to evaluate allometric growth and R^2 values were collected to determine correlation. Each comparison was then reviewed to extract any significance.

Results

The holdfast measurements do not correlate remotely to any other part of the organism's growth, indicating that the holdfast is controlled largely by environmental factors and should therefore not be used to determine growth patterns or delineate species. It is likely that the holdfast is responding to water velocity and the type of substrate to which it was attached (Brett et al., 1997; Thomka et al., 2016; Sheffield and Sumrall, 2017). Based on the results of this analysis (Fig. 3, Fig. 4), it is clear that the holdfast growth is not correlated with the ontogeny of the rest of the organism.

The width of the mouth (measured from BC-DE interray) is increasing at a faster rate than the length (A ambulacrum to CD interray), indicating negative allometry of the width of the mouth (Fig. 5). The ambulacra are growing faster than the thecal width, indicating positive allometry of ambulacral growth (Fig. 6). The length of brachioles are also growing with positive allometry with respect to the length of mouth and the thecal width (Fig. 7, Fig. 8). The number of brachioles does not chnge throughout ontogeny, however; all brachioles appear to be present at the earliest stages represented in this collection.

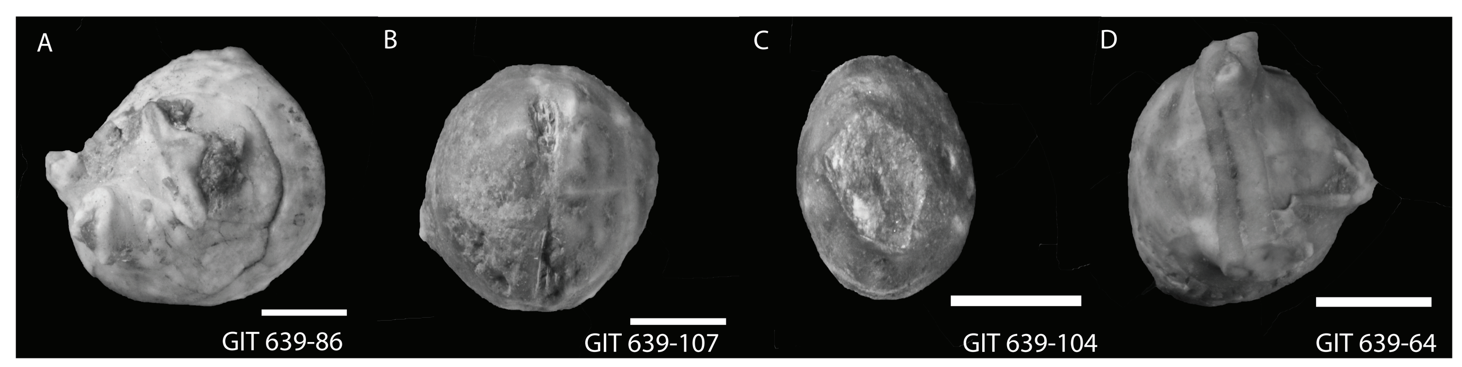

Fig. 2. The holdfast varies widely across specimens within the collection; this indicates that the shape of the holdfast is dictated by environmental factors, as opposed to ontogeny. A, B. Narrow slit for holdfast. C. Wide attachment base. D. Narrow slit that extends the length of the theca. The change in size of the holdfast is likely due to the type of substrate to which it is attached. Scale bars=1cm.

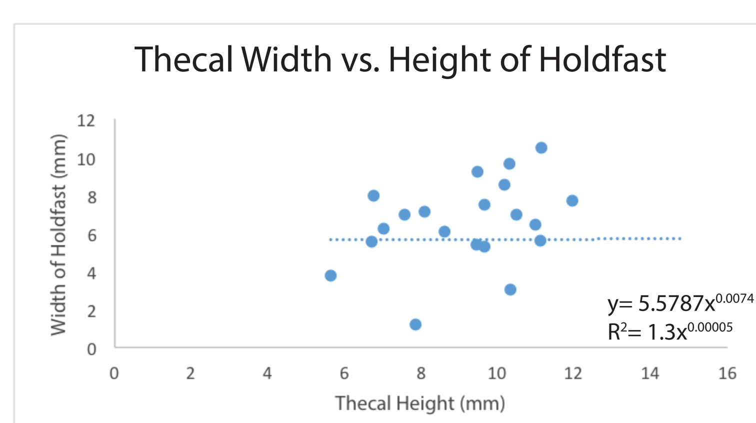

Fig. 3. The length and width of the holdfast show no correlation to one another, indicating that changes in shape are not ontogenetic.

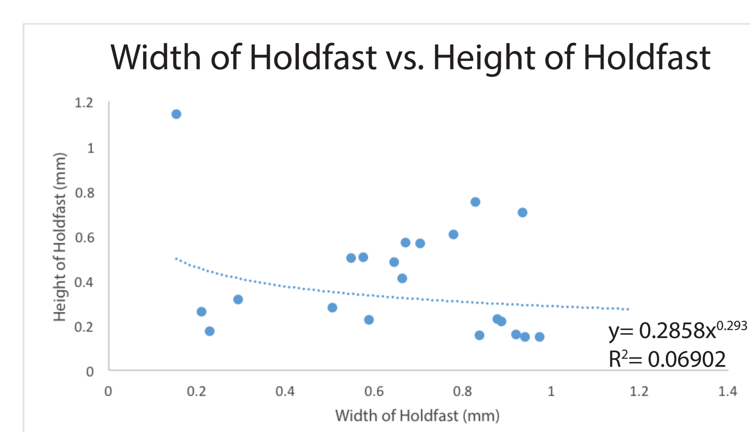

Fig. 4. The width and length of the holdfast show no correlation of growth, indicating that changes in shape are not ontogenetic.

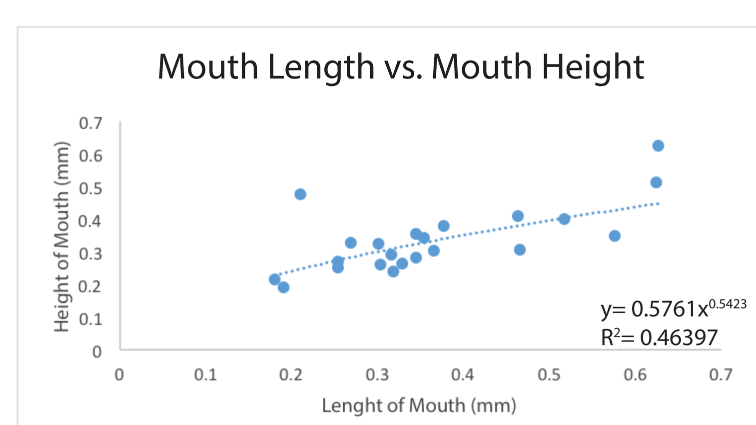

Fig. 5. The width of the mouth is increasing faster than the length of the mouth (i.e., growing with negative allometry)

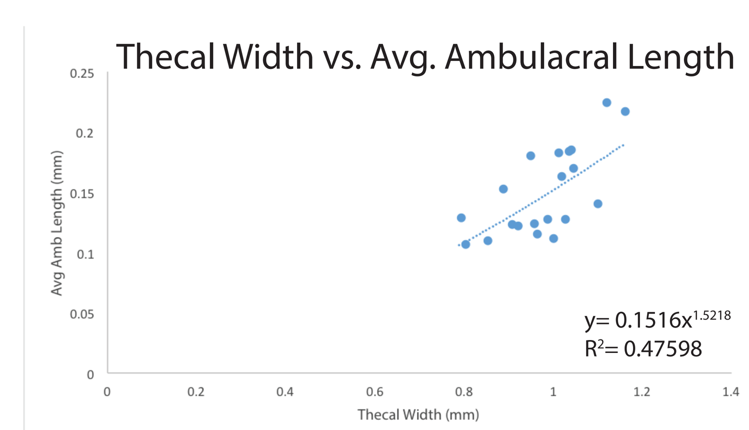

Fig. 6. The average length of the ambulacra is increasing faster than the thecal width (i.e., growing with positive allometry)

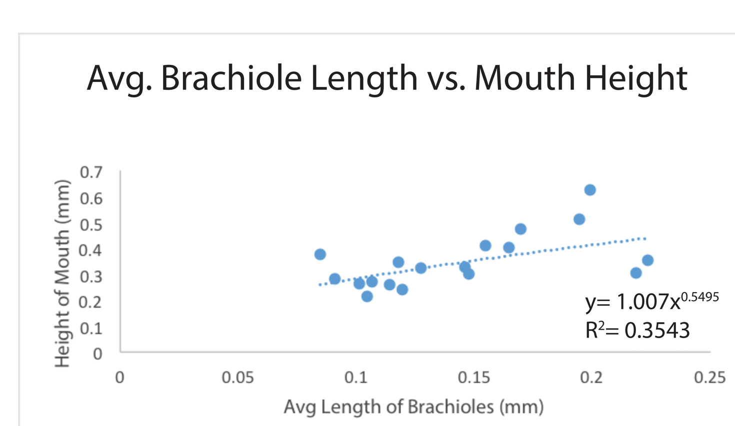

Fig. 7. The average length of the brachioles is increasing faster than the length of the mouth (i.e., growing with negative allometry)

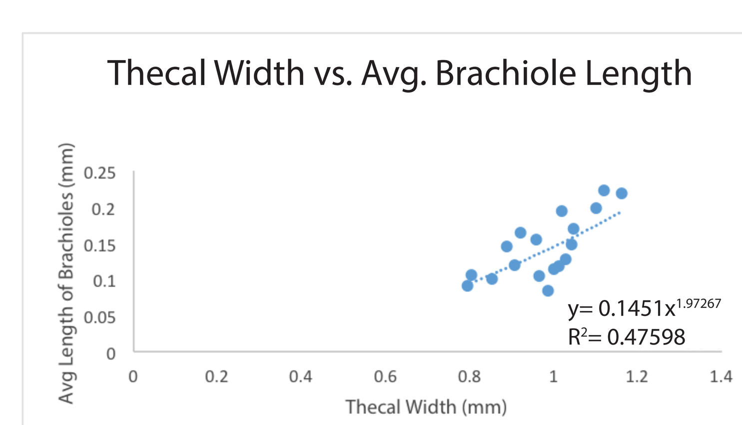

Fig. 8. The average length of the brachioles is increasing faster than the width of the theca (i.e., growing with positive allometry)

Taphonomy

Taphonomic overprinting affects our ability to assess ontogenetic changes. While diploporitans are usually more likely to be preserved than other types of echinoderms (Brett et al., 1997), diploporitans are still not preserved in high numbers and they often show extensive weathering and disarticulation of plates. In this particular collection, some thecae were also noticeably compacted. These compacted thecae that would prevent accurate measurements were not utilized in this study. Taphonomic processes also caused the majority of plate sutures to be worn away. Because of this, measurements directly involving plate growth were not possible for the majority of specimens and therefore not included in this analysis. Cover plates of the peristome and periproct, along with gonopore and hydropore, were not preserved in any specimen.

Heterochrony

Heterochrony, the developmental change in timing of ontogenetic events, has been recognized in a number of echinoderm clades (Sumrall and Wray, 2007). As heterochrony can only be determined by looking at the evolutionary trends of taxa, two species of *Eucystis* were compared, *E. angelini* (Fig. 9) and *E. quadrangularis* (Fig. 10). *E. quadrangularis* shows a paedomorphic reduction of the A ambulacrum, which indicates that there was a change in the evolutionary trends of this taxon to retain juvenile characteristics (i.e., the loss of the A ambulacrum

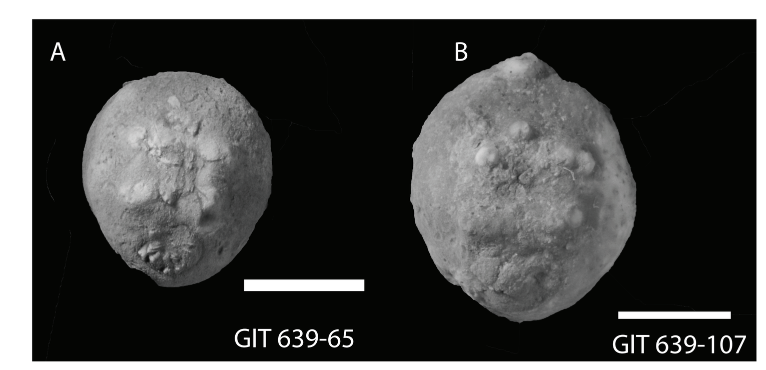

Fig. 9. Two oral areas of specimens of E. angelini that show five ambulacra, the plesiomorphic condition for diploporitan echinoderms. Scale bars=1cm.

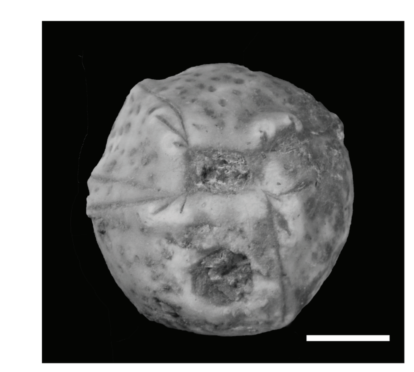

Fig. 10. GIT 639-17. *E. quadrangularis* shows a paedomorphic reduction of the A ambulacrum. Scale bar=1cm

Discussion

Eucystis angelini grows with a combination of both positive and negative allometry. The length of ambulacra increased faster than the size of the theca; this is most likely for more efficient food capture. The brachioles are all present at the smallest ontogenetic stage in the sample. It does not apper that the brachioles are being added as the organism matured, but growing in size. The increase in size is most likely also related to effecient food capture. Measurements of the holdfast showed to be irrelevant to growth patterns and showed no correlation to any of the other variables. *E. quadrangularis* shows paedomorphic heterochrony with the reduction of the A ambulacrum. The width of the mouth grows faster than the length which could allow for more efficient ingestion food capture.

References & Acknowledgments

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