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GROWTH AND FORM OF THREE SPECIES OF PENTREMITES (ECHINODERMATA: BLASTOIDEA)

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ABSTRACT

Three species of *Pentremites*, *P. godoni* (Defrance) Hall, *P. pyriformis* Say, and *P. robustus* Lyon, were studied to determine changes in thecal morphology during ontogeny. These morphological changes were probably related to changing food-gathering requirements during growth. *Pentremites godoni* and *Pentremites robustus* show an allometric growth pattern, accompanied by a significant ontogenetic change in thecal form, whereas in *Pentremites pyriformis*, also demonstrative of allometric growth, there appears less ontogenetic change in thecal form. Increases in ambulacral length and width, relative to increases in thecal volume, are inferred to enhance food-gathering and respiratory functions of the organism. Although all three species show similar ontogenetic patterns, the increasing thecal volume of *P. robustus* relative to increases in ambulacral length is greater than that for either *P. godoni* or *P. pyriformis*. *P. robustus* was apparently approaching the maximum size a *Pentremites* could attain and still maintain a favorable area/volume ratio.

INTRODUCTION

Pentremites is an extinct, Carboniferous, marine echinoderm, having a theca composed of thirteen main plates and numerous accessory plates (Galloway and Kaska, 1957) (Figure 1). At the proximal end of the theca are three outwardly flaring basal plates attached to a round, jointed stem, composed of numerous plates or columnals. The stem was attached to a stable substrate. Above the basal plates are the radials, a circlet of five deeply forked plates. Alternating with the radial plates are elliptical areas called ambulacra. The ambulacra are traversed by shallow grooves which functioned in the movement of water and nutrients, and are bordered by slender food-gathering appendages termed brachioles. The ambulacra also functioned in respiration; a thin-walled respiratory structure

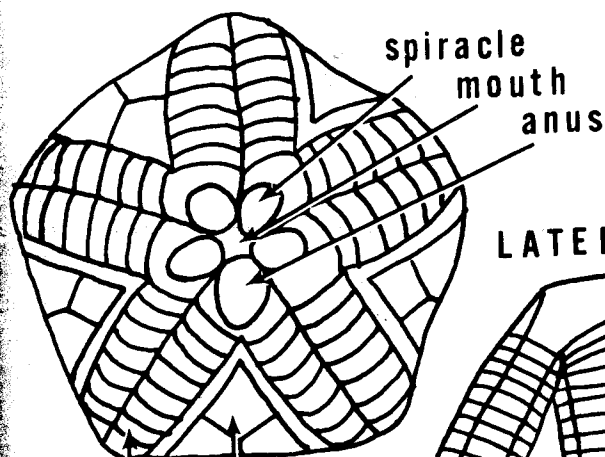
(hydrospire) was infolded beneath the ambulacral border, and pores along the ambulacral border served as an inlet to the respiratory system. The region delimited by the ambulacral borders, tangentially joining the contact zone of every two plates, is the interambulacrum. The theca consists of five quadrangular plates forming the uppermost portion of the theca consists of five quadrangular terradial deltoids. At the distal end of each deltoid is a spiracle which served as an inlet for the water vascular system. One of five spiracles is considerably larger than the others, being a combined spiracle and hydrospire (Raup and Stanley, 1971; Moore, Lalicker, and Fischer, 1952). The theca of a *Pentremites* is divisible into two regions, the vault and the pelvis. The vault is that portion consisting of the basal end of the ambulacra distally to the oral end of the theca. The pelvis is the area extending from the oral end of the ambulacra to the point of attachment.

The length and area of the ambulacra are related to the ability of individuals of *Pentremites* to gather food. The ambulacra are the attachment sites for the brachioles which filtered the surrounding water for food (Moore, Lalicker, and Fischer, 1952). Presumably, wider ambulacra would produce a more efficient food-gathering system by increasing the area covered by the filtration fan. The ability to gather food is related to the length of the ambulacra; a longer ambulacrum possesses more brachioles. Larger ambulacra may have increased efficiency in respiration, by increasing the volume of water the hydrospires could process.

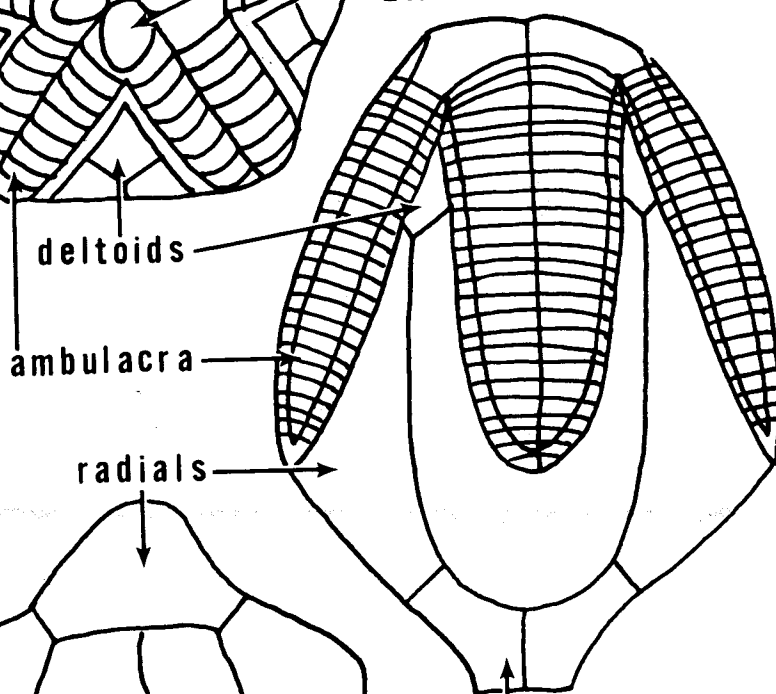
Purpose

This study was initiated to ascertain the functional morphology of three species of *Pentremites*: *P. godoni* (Defrance) Hall (1819), *P. pyriformis* Say (1825), and *P. robustus* Lyon (1860); to compare their growth forms; and to develop a technique that would be useful for distinguishing blastoid species in other genera. The habitats of

ORAL VIEW



LATERAL VIEW



BASAL VIEW

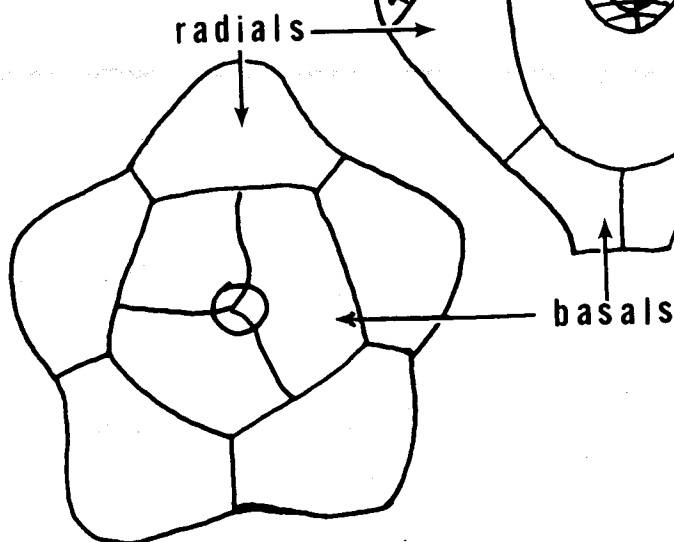


Figure 1—Oral, basal, and lateral views of a typical *Pentremites*. (Redrawn from Raup and Stanley, 1971.)

the three species were probably similar, as the genus is inferred to have lived in moderately high energy environments of shallow water (5–20m), and to have been capable of withstanding moderate influxes of fine-grained clastics (Macurda, Waters, and Horowitz, 1979).

Materials and Methods

Pentremites robustus (Plate 1, fig. 1) has a globular, godoniform theca, concave ambulacra, slightly concave interambulacra, and a vault/pelvis ratio ranging between 2.5–4. The adults are large, ranging from 46–50 mm in length and 43–45 mm in width. The specimens used in this study are from the Moulton Quarry in Lawrence County, Alabama.

Pentremites pyriformis (Plate 1, fig. 2) possess a pyriform theca, flat to slightly convex ambulacra, flat to slightly concave interambulacra, and a vault/pelvis ratio equal to 0.9–1. Adults are typically 20–27 mm in length and 14–26 mm in width. The specimens used in this study were collected near Fox Trap Creek in Colbert County, Alabama.

Pentremites godoni (Plate 1, fig. 3) possesses an ovate, godoniform calyx, slightly convex ambulacra, concave interambulacra, and a vault/pelvis ratio ranging between 4–8. Adults are typically about 18 mm in length and 15 mm in width. The specimens used in this study were collected in Huntsville, Madison County, Alabama.

Measurements of three characters were made on each specimen: length of the ambulacra, total surface area of the ambulacra, and volume of the theca. Ambulacral length was measured with vernier calipers. It was assumed that each ambulacral area approximated an ellipse, and by using the formula, $\text{Area} = 5/4 ab$, where a is the length of an ambulacrum and b is the width of an ambulacrum, the ambulacral area was calculated. Volume was determined by immersing each specimen in a graduated cylinder and noting its displacement. A five percent soap solution was used to reduce the meniscus and minimize possible error in volumetric determination.

For each species, volume was plotted against ambulacral length and ambulacral area (Figures 2a, 2b). When the points are

plotted on logarithmic paper, the trends of the three species form straight lines. The equation describing the lines is: $\log y = a \log x + \log b$. The exponent a is the slope of the line when graphed on logarithmic paper and indicates that the variables x and y increase at different rates of growth, but that the ratio of these rates is constant.

The method chosen to illustrate the growth gradient is by the growth transformation diagrams of Thompson (1961). The method consists of laying a grid over the diagram of a juvenile of each species and drawing the lines on the grid at distinct reference points. The points chosen in this study were: (1) the oral end of the theca, (2) the upper extremity of the deltoids, (3) the lower extremity of the deltoids, (4) the lower extremes of the ambulacra, (5) the lower extremes of the radials, and (6) the aboral end of the theca. The grid was then redrawn on a diagram of an adult specimen of each species, with the lines again drawn at the same reference points. The difference in the spacing of the lines illustrates different rates of growth between the various plates of the theca (Figures 3a, 3b, 3c).

RESULTS

In the case where x equals ambulacral length and y equals volume, a slope of 1.5 shows isometry (Huxley, 1932). With isometric growth, increases in length are keeping up with increases in volume. When x equals ambulacral area and y equals volume, a value of 1.5 shows isometry (Huxley, 1932). Figure 2a shows the plot of volume against ambulacral length and values of 1.65, 1.84, and 2.58 for *Pentremites pyriformis* (a), *P. godoni* (b), and *P. robustus* (c), respectively. In *P. pyriformis* and *P. godoni*, the increases in length exceed increases in volume. This is also true of *P. robustus*, but to a lesser extent. Therefore, *P. robustus* has a greater increase in volume per unit increase in ambulacral length than either of the other two species. Figure 2b shows the plot of volume against ambulacral area and values of 0.961, 1.22, and 1.598 for *P. pyriformis* (a), *P. godoni* (b), and *P. robustus* (c), respectively. For *P. pyriformis* and *P. godoni*, the ambulacral area increases faster than volume. However, volume in *P. robustus* increases slightly faster than ambulacral area.

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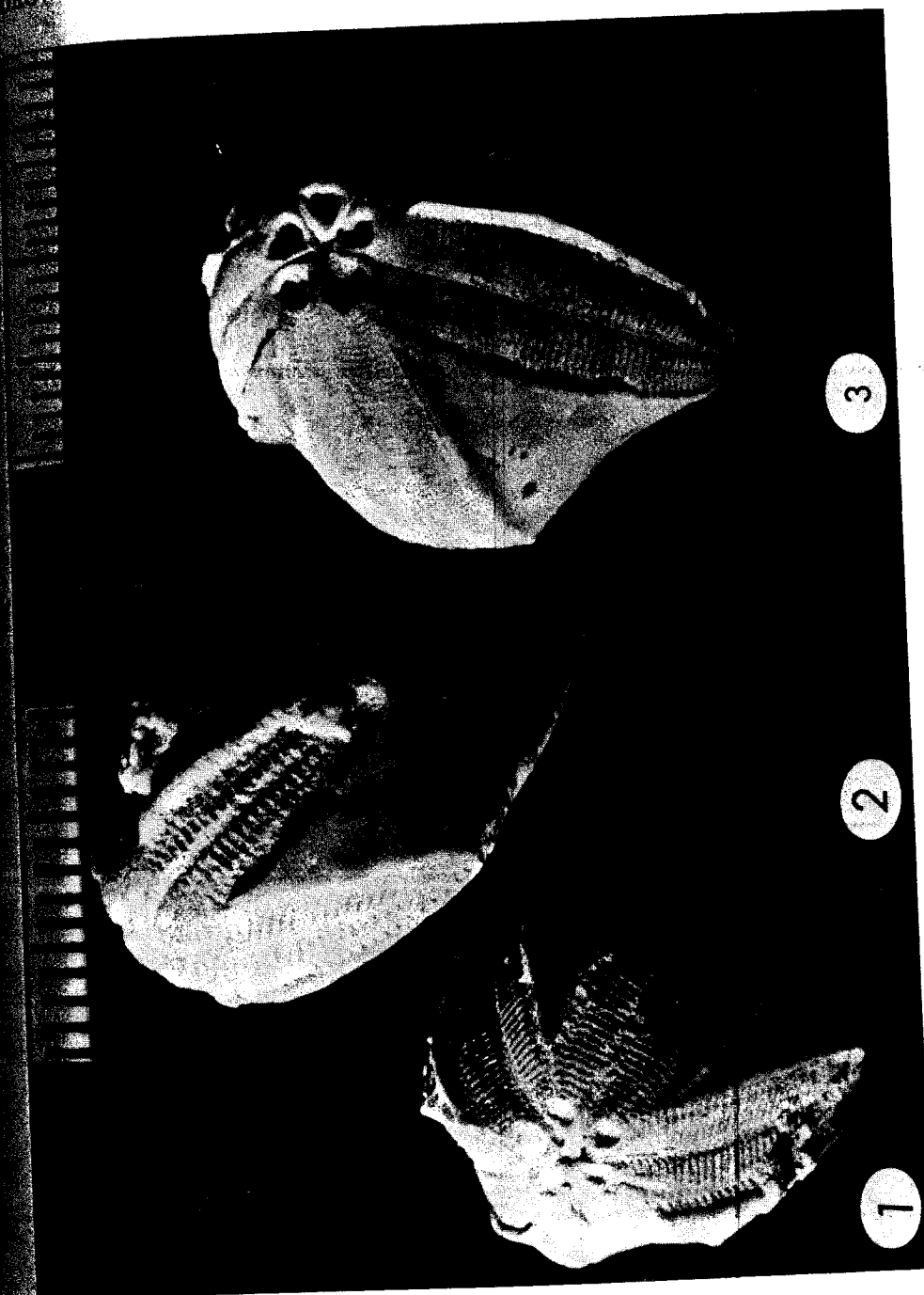


Plate 1—*Pentremites godoni* (fig. 1), *Pentremites pyriformis* (fig. 2), and *Pentremites robustus* (fig. 3).

The equation of simple allometry is a convenient way of summarizing the growth of a part of an organism to the whole of the organism (Gould, 1966). In the case of the three species of *Pentremites*, *P. pyriformis* and *P. godoni* show essentially the same allometric equation. The equation indicates that the ability of an individual *Pentremites* to grow and thrive is related to its ability to maintain a favorable ratio of increase in ambulacral area, relative to increasing volume. The fact that these species are functionally similar but morphologically different probably indicates that morphology is of secondary importance to the area of the ambulacra relative to volume, and probably only served to keep the viscera enclosed.

Although *Pentremites robustus* generally follows the pattern of *P. godoni* and *P. pyriformis*, it does differ. Growth relative to an increase in ambulacral length is greater than in the other two species, and its volume appears to increase more rapidly than ambulacral area. This suggests that *P. robustus* was nearing the maximum size a *Pentremites* could attain and still maintain a favorable area/volume ratio. One of the ways animals compensate for a less favorable area/volume ratio is to incorporate inorganic materials into their volume, thereby cutting down on the volume the animal actually occupies. Specimens of *P. robustus* from the Moulton Quarry exhibit abnormally thick thecal plates that may represent a natural mechanism to reduce the animal's internal volume.

The morphological changes that occur during ontogeny of individuals within the three species are illustrated by the growth transformation diagrams in Figures 3a, 3b, and 3c. The differential spacing of the reference lines illustrates the great increase in vault and decrease in pelvis in *Pentremites godoni* (Figure 3b) and *P. robustus* (Figure 3c) during ontogeny. *P. pyriformis* (Figure 3a) maintains about the same relative proportions throughout growth.

DISCUSSION

If geometrical similarity is maintained as size increases, any series of objects will exhibit continually decreasing ratios of surface area to volume. This is a simple con-

sequence of geometry. Area increases as the square of the linear dimensions, whereas volume increases as the cube of the linear dimensions. Constant area to volume ratios, an adaptive necessity for many organisms, can only be maintained by altering shape. The growth transformations show that *Pentremites* changed shape during ontogeny in response to the greater food demands of the growing organism. In *P. pyriformis* and *P. godoni*, ambulacral length and ambulacral area increase faster than thecal volume. Although these two species show essentially the same allometric equation, morphological changes within the same two species differ. Although *P. pyriformis* maintains approximately the same vault/pelvis ratio throughout growth, there is a great increase in vault and decrease in pelvis in specimens of *P. godoni*. Specimens of *P. robustus* also show a large increase in vault and decrease in pelvis. Although ambulacral length is increasing slightly faster than thecal volume, the unit increases are not as large as for *P. pyriformis* and *P. godoni*. In *P. robustus*, thecal volume is increasing slightly faster than ambulacral area. In all three species, changes in the shape of the theca occurring during ontogenetic development are of secondary importance relative to the ratio of ambulacral area to total thecal volume.

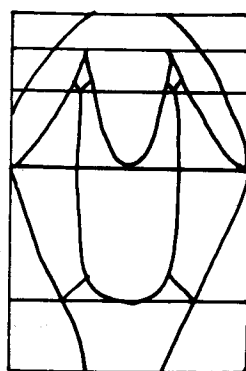
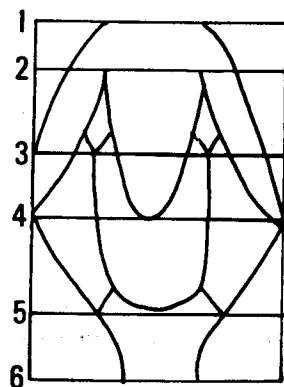
Since anatomical parameters of individual *Pentremites* underwent considerable changes during their growth, application of this technique for studying ontogenetic changes and functional morphology in *Pentremites* may help remove much of the taxonomic confusion prevalent in this group. The use of growth patterns as taxonomic criteria, as demonstrated by Macurda (1975), will perhaps serve to eliminate many of the mistaken taxonomic distinctions of many species of *Pentremites* as well as other blastoid genera.

ACKNOWLEDGMENTS

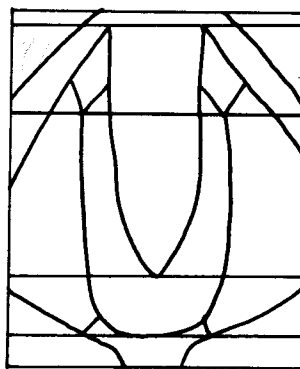
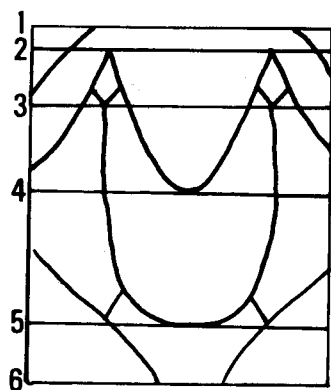
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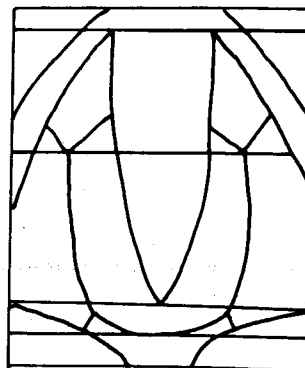
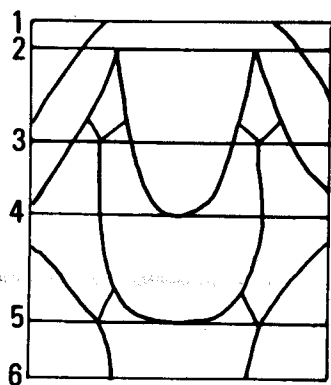
Figure 2— a. Plot of ambulacral length (mm) vs. volume (ml) for *P. pyriformis* (a), *P. godoni* (b), and *P. robustus* (c). b. Plot of ambulacral area (mm²) vs. volume (ml) for *P. pyriformis* (a), *P. godoni* (b), and *P. robustus* (c).



a



b



c

Figure 3— a. Growth transformation diagrams of a juvenile (left) and an adult (right) of *P. pyriformis*.
 b. Growth transformation diagrams of a juvenile (left) and an adult (right) of *P. godoni*.
 c. Growth transformation diagrams of a juvenile (left) and an adult (right) of *P. robustus*.

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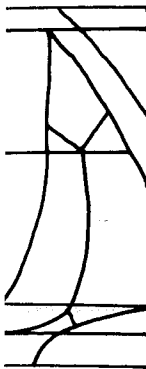
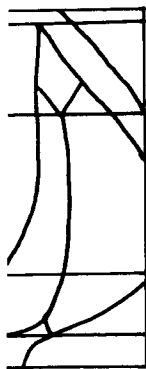
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