Zootaxa 4052 (2): 151–179
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4052.2.1
http://zoobank.org/urn:lsid:zoobank.org:pub:3D92BEC3-F344-470F-AE21-94978465F1EA

Holistic morphometric analysis of growth of the sand dollar *Echinarachnius parma* (Echinodermata:Echinoidea:Clypeasteroida)

LOUIS G. ZACHOS
Department of Geology and Geological Engineering, University of Mississippi, University, MS 38677, USA.
E-mail: lgzachos@olemiss.edu

Abstract

Holistic morphometrics is a term implying complete shape characterization of all of the structural parts of an organism. The skeleton of an echinoid is comprised of hundreds of individual plates arranged in a closed 3-dimensional mosaic forming the test. GIS software and techniques were used to generate topologically correct digital models of an ontogenetic series of specimens of the sand dollar echinoid *Echinarachnius parma*. Plate growth can be considered in proportion to overall skeleton growth, resulting in a linear model of relative growth. Alternatively, separate logistic equations can be fit to the ontogenetic series of homologous plate areas using nonlinear least squares regression to result in a model for instantaneous growth. The linear and logistic parameters of the models describe the allometric growth of plates from different viewpoints. Growth is shown to fall into characteristic patterns defining distinct plate growth domains associated with development of the imago (larval) skeleton just prior to metamorphosis, early growth associated with expansion of the corona and fold-over (forming the flattened body form), juvenile growth and formation of petals, and adult growth. Functions of growth, plate translocation, plate juxtaposition between aboral and oral surfaces, and relationships with internal buttressing are quantified. Results offer explanations for general skeletal symmetry, distinction between ambulacral and interambulacral growth, the relationship of growth to internal buttressing, existence of a distinct petalodium, and anterior-posterior asymmetry during development. The parametric values of growth functions derived from the results are a basis for computational modeling of growth and development in sand dollars.

Key words: Skeleton, GIS, morphology, ontogeny, allometry, computational model

Introduction

The skeleton or test of the sand dollar echinoid *Echinarachnius parma* shows nearly symmetrical growth, with simple petals (flush, lacking demiplates or occluded plates) and no lunules. These characteristics make the species an ideal model for a study of growth and development of the skeleton. At metamorphosis, the skeleton of *E. parma* may have as few as 38 plates, but as a fully mature adult the number can exceed 1000 plates. The flattened form of sand dollars results in a restricted number of plates (about 100) on the ventral or oral side, so that nearly all plates are added to the dorsal or aboral side. Growth of the animal requires growth of the individual plates concomitant with addition of new plates within constraints of overall body form. This study uses a holistic approach to incorporate measurements of plate growth throughout ontogeny from juvenile through mature adult stages, based on detailed measurements of dimension and location of all of the plates for all specimens in the series. Plate homology among individuals is based on plate cohort number. The set of basicoronal plates (those surrounding the peristome) are the first cohort and cohort number increases monotonically for plates in each of the 20 columns. Plate growth can be considered in proportion to overall skeleton growth, resulting in a linear model of growth. Alternatively, separate logistic equations can be fit to the ontogenetic series of homologous plate areas using nonlinear least squares regression. The logistic and linear coefficients describe the allometric growth of plates from different viewpoints, and growth is shown to fall into characteristic patterns defining distinct plate growth domains. Major stages of development can be divided into development of the imago skeleton just prior to metamorphosis, early growth associated with expansion of the corona and fold-over (forming the flattened body form), juvenile

Accepted by M. Eleaume: 2 Nov. 2015; published: 2 Dec. 2015