Classifying echinoid skeleton models: testing ideas about growth and form

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Abstract.—Theoretical morphology is the scientific field in which researchers model organism growth and form. The field is developed well in studies on skeletons, especially shells. Researchers have contributed echinoid skeleton models to the field, but these have yet to be recognized collectively. We present herein the first comprehensive review for echinoid skeleton models in theoretical morphology. We apply a phylogenetic systematic analysis to those models, use the resulting consensus cladogram to classify and interrelate the models in an analogy in which they are likened to fossil specimens in a biostratigraphic record, and utilize the biostratigraphic metaphor to define trends within theoretical morphology as it applies to echinoid skeleton models.

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Introduction

Philosophers and historians classically describe scientific progress as transpiring either incrementally, by falsifying hypotheses (e.g., Popper 1987), or revolutionarily, by replacing paradigms (e.g., Kuhn 1970). These two extreme perspectives are analogous to the now classical gradualism and punctuated equilibrium camps in evolutionary science, gradualism entailing that organisms evolve steadily over long geological time periods (e.g., Darwin 1859) and punctuated equilibrium entailing that organisms evolve in bursts over short geological time periods, followed by stasis (e.g., Gould and Eldredge 1977).

This association between descriptions of how science progresses and how organisms evolve is more than coincidental. Natural selection has been invoked as the process by which science progresses (e.g., Campbell 1974; Hull 1988), and the relationships among research contributions within a scientific field may be analyzed from an evolutionary perspective (e.g., Stone 1996).

Theoretical morphology may be defined generally as the scientific field in which models are developed to explain and describe organism growth and form (Thompson 1917). In modern theoretical morphology, models usually involve mathematics, computation, and graphical simulation (e.g., Raup 1966, 1968). Analyses often are presented with reference to morphological spaces, or "morphospaces," mathematical spaces with axes delineated by parameters describing growth or form and in which each point represents the morphology for a taxon or organism (or part thereof). Researchers identify regions in those morphospaces that have been unoccupied and occupied (or would be) by organisms (extinct or extant) and erect hypotheses on the basis of distributions that are observed. The hypotheses lead to experiments, which can be used to test and refine or erect new hypotheses. In this manner, theoretical morphology epitomizes the interplay ("reciprocating illumination" sensu Hennig 1966) that generally relates theory and practice in science.

Stone (1996) has reviewed one particularly well developed class within theoretical morphology, theoretical conchology (i.e., theoretical morphology as it applies to shells), by considering models as species and conducting a parsimony-based, phylogenetic systematic analysis (Stone 1996). By conducting a distance-based, phenetic analysis on the morphospaces themselves, Stone (1997) also has reviewed how morphospaces generally have been used to explore biological systems. And McGhee (1999), in a book, reviewed the entire field itself.

A more-recent review for the field involved a hybrid approach, which combined parsimony-based and distance-based analyses (Dera et al. 2008). Absent from that analytical review were studies in theoretical morphology as it applies to echinoid (Echinodermata: Echinoidea, e.g., sea urchins, sand dollars, and heart urchins) skeletons. We complement that review by conducting a parsimony-based analysis on echinoid skeleton models, then ''grounding'' the results by considering them from a descriptive, distance-based analysis in which the models metaphorically are likened to fossil specimens in a biostratigraphic record.

Morphological Models

A morphological model is a construct that represents organism growth or form. Morphological models may be used to explain and describe observed patterns (different components or structures among organisms) or processes (changes through ontogeny or evolution). For instance, using shell geometry, related mathematical equations, and a computer program, Raup (1966) presented a three-dimensional ''morphospace'' in which shell forms were represented. Some regions in the morphospace were empty, presumably as a consequence of functional constraints (e.g., impeding hinges between articulating bivalve shells).

To create a biologically meaningful morphological model, a thorough understanding about morphogenesis is necessary; merely duplicating appearances is insufficient. Morphologies may be considered from different approaches, and multiple models may be derived to explain and describe growth or form for the same organisms. One approach, mechanistic modeling, involves using process-based principles, such as those associated with genetics or physiology. Another approach, dynamic modeling, involves using pattern-based principles, such as those associated with mathematics or physics. For instance, Stone (1996) identified two main approaches to theoretical conchology: one in which shell growth was primary, thereby involving processes associated with shell accretion at a mantle edge, and another in which form was primary, thereby involving patterns associated with shell architecture.

Contemporary theoretical morphologists may decide whether to adopt a mechanistic, dynamic, or mixed approach. From an echinoid skeleton modeling perspective, researchers adopting a mechanistic approach can utilize data from the sea urchin genome project (Sea Urchin Genome Sequencing Consortium 2006) or could represent factors underlying processes such as gene expressions, signal transductions, growth-factor interactions, hormone concentrations, and developmental pathways. Researchers adopting a dynamic approach can utilize data derived on the basis of mathematical or physical principles (e.g., geometry or energetics [Raup 1968; Ellers 1993; Abou Chakra and Stone 2008, 2011]) or could represent factors underlying patterns such as genotype-phenotype maps, material depositions, structural constraints, phylogenetic histories, or adaptations.

Echinoid Tests

Echinoderms, particularly echinoids, with the appealing and intricate plate arrangement and pentamerous symmetry in their skeletons, have evolved processes and patterns that have puzzled morphologists for centuries (Hyman 1955). Skeleton plate patterns and shapes have proven challenging to explain and describe completely on the basis of any one approach or principle.

Echinoid Test Structure.—Echinoids possess transient skeletons as larvae and permanent skeletons, or tests (Fig. 1), as adults. Generally, permanent skeletons may be classified on the basis of whether they change after initial formation (Vermeij 1970). Skeletons that remain unchanged after formation are immutable (e.g., brachiopod shells), and skeletons that allow morphological changes to occur by peripheral accretion, resorption, and growth are modifiable (Vermeij 1970). Echinoid tests are modifiable; morphological changes during ontogeny are exceedingly complex, because skeletal tissue can be deleted, altered, or elaborated (Jackson 1912; Vermeij 1970). Each echinoid test is an endoskeleton within a three-layered body wall comprising an external epidermis, middle dermis occupied by the endoskeleton, and coelomic lining (Hyman 1955).
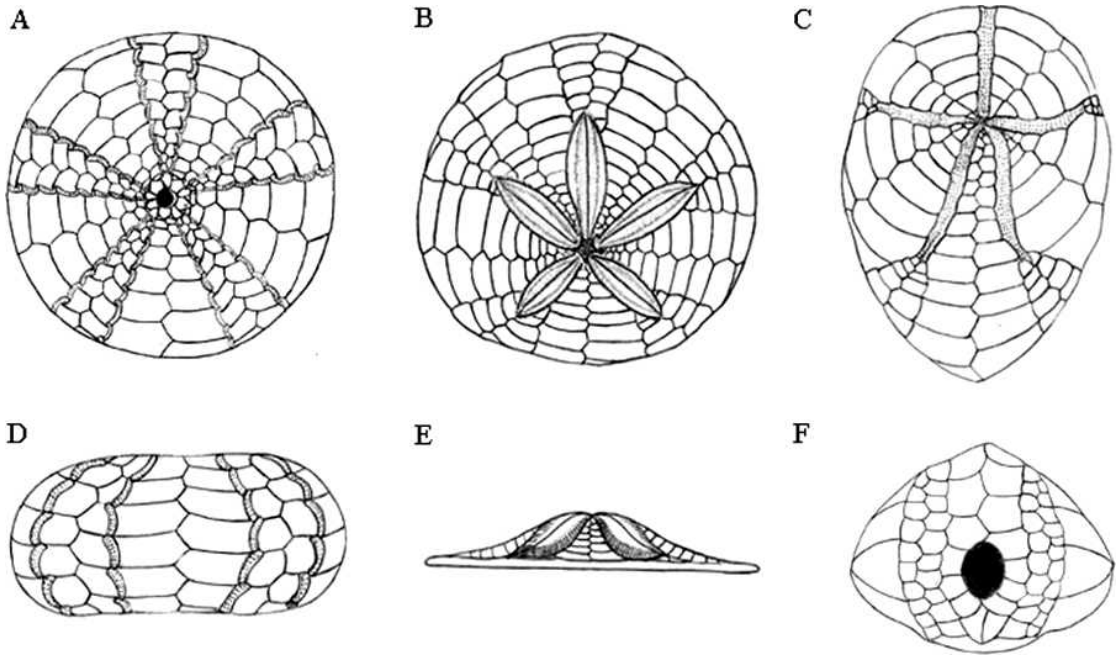
FIGURE 1. Echinoid tests (illustrations representing three species). A, Regular echinoid (sea urchin, *Strongylocentrotus franciscanus*). B, C, Irregular echinoids—a clypeasteroid (sand dollar, *Dendraster excentricus*) and a spatangoid (heart urchin, *Brissus unicolor*), respectively. D, E, F, *S. franciscanus*, *D. excentricus*, and *B. unicolor*, respectively, in lateral view.

Echinoid tests are constructed from adjoining calcium carbonate plates (Jensen 1972; Smith 1980) and may be divided into three regions on the basis of plate characteristics: the apical system, corona, and peristome. The apical system comprises ocular plates and genital plates; in regular echinoids and early irregular echinoids, the apical system also contains the periproct (Smith 1984). The corona, the entire test minus the apical system, contains ambulacral plates and interambulacral plates. New ambulacral and interambulacral plates are inserted contiguous to ocular plates (Jackson 1912; Gordon 1926, 1927; David and Mooi 1996). The peristome contains buccal (mouth) plates and sometimes primordial ambulacral plates (Hyman 1955; Smith 1984).

Echinoid Test Ontogeny.—Echinoid test ontogeny can be divided into five biological processes: visceral growth, plate addition, plate growth, plate gapping, and plate interaction. Visceral growth is the process in which the internal membrane and structures change size, altering internal pressure (Deutler 1926; Ellers and Telford 1992); plate addition involves the insertion of new plates at the apical system, adjacent to ocular plates (Jackson 1912); plate

growth is the process in which plates are accreted or resorbed peripherally (Märkel 1981); plate gapping involves the separation of plates from one another, creating spaces that allow plate growth (Dafni 1986; Johnson et al. 2002); and plate interaction is the process by which connections between adjacent plates affect plate arrangements and morphologies.

Echinoid Test Models

Echinoid test ontogeny has been scrutinized by many researchers (e.g., Lovén 1874; Jackson 1912; Deutler 1926; Gordon 1926, 1927; Pearse and Pearse 1975; Smith 1980, 1984; Märkel 1981; Dafni 1986; Ebert 1988; Philippi and Nachtigall 1996) whose works ultimately influenced the theoretical morphologists who produced the nine echinoid test models that have been published: Thompson (1917), Moss and Meehan (1968), Raup (1968), Seilacher (1979), Telford (1985, 1994), Baron (1990, 1991), Ellers (1993), Zachos (2006, 2007a,b, 2009a,b), and Abou Chakra and Stone (2008, 2011).

Thompson.—Thompson (1917) compared the shapes that are exhibited by regular echinoids to shapes assumed by liquid drops subjected to gravity while resting on flat surfaces. Drop

shapes result from forces that are associated with surface tension balancing a linear, positive internal pressure gradient. Thompson considered entire tests as plastic entities that grow incrementally, allowing movement between calcareous plates. Along with gravity, test shapes are effected by forces that are exerted by tube feet adhering to surfaces. Tube feet impart these forces symmetrically, spreading in all directions and resulting in downward slopes.

Moss and Meehan.—Deutler (1926) proposed that any perceived downward ''shift'' that plates convey during echinoid test ontogeny is only apparent and relative to an enlarging test rather than genuine migration. Moss and Meehan (1968) expanded on Deutler's idea and considered echinoid test ontogeny as analogous to mammalian cranial expansion. They hypothesized that test ontogeny is induced by ''expansive forces''; the primary growth associated with expanding internal visceral tissues is the impetus for test growth, causing gaps between plates. Plates grow to fill the space created. They proposed a conceptual ''internal plane of registration,'' which depicts the relative positions among the apical system, corona, and peristome. Concurring with Deutler's views, Moss and Meehan proposed that test expansion causes the adoral spatial displacement that is imparted to plates.

Raup.—Elaborating on a soap-bubble analogy that was proposed originally by Thompson (1917), Raup (1968) considered plate addition, plate growth, and plate interaction as the major components in test growth. Raup demonstrated experimentally that soap-bubble interactions confined to approximately two dimensions (i.e., between two glass plates) can be used as a model for producing and interpreting echinoid plate patterns. He extrapolated close-packing pattern similarities as evidence for sutural compression, which limits plate growth and consequently determines plate shape.

Raup (1968) transformed his conceptual model into a computational model that involved plate addition and plate growth. Plate addition was simulated by using a logistic function. Plate growth was divided into initial growth, meridional growth, negative growth,

and distal growth; to address these divisions, Raup chose a parabolic function, estimated from growth data.

The computer program that Raup (1968) developed graphically simulated a growing interambulacral column, starting from a new plate with zero size. Plate margins were depicted with straight lines and angles between boundaries were assumed to be coequal. With the computer program, Raup explored the effect on plate interactions under different growth parameters.

Seilacher.—To describe the morphological differences among echinoids, Seilacher (1979) considered tests as mineralized pneu structures with internal tethering, tensional spheres supported internally by liquid pressure, which grow when internal pressures exceed external surface tensions. Seilacher referred to internal tethering to explain the irregularities (flattening, dimples, depressions, and pouches) that are observed in test shapes that characterize irregular echinoids and proposed that individual plate growth differences produce changes in column arrangement and ultimately in test morphologies.

Telford.—On the basis of the observation that domes provide the greatest strength for rigid structures, Telford (1985) hypothesized that echinoid tests are constructed to resist external forces such as tension and compression. Structural strength is greater in a high dome than a low dome (Lawrence 1987). For echinoids, this difference might have its origin in function, growth rate, support, and protection (Lawrence 1987).

Telford (1985) conducted a biomechanic analysis and, using simple membrane theory and statistical analysis, described how mechanical design facilitated adaptation. The analysis showed that echinoids are built to accommodate compressive and tensile stresses resulting from a variety of membrane and arch action combinations. Using structural principles involved in dome and arch construction, Telford proposed a model for echinoid tests.

Subsequently Telford (1994) proposed a three-dimensional model for echinoid tests, which elaborated on Raup's (1968) two-dimensional model by linking plate columns. The model was proposed to describe morphogenesis

quantitatively and explore unobserved as well as observed shapes.

Baron.—Baron (1990) proposed that test shapes could be explained by considering a variety of heritable characteristics and environmental influences that mediate growth, suggesting that regular echinoid tests were precluded from becoming flat. Baron (1991) used finite element analysis to elucidate how regular echinoid tests responded under different force loads (repeated subsequently by Philippi and Nachtigall 1996). The results obtained were consistent with the hypothesis that changes in height (H) and diameter (D) tend toward the fixed ratio H:D ≈ 0.55 (Ebert 1988; Baron 1990).

Baron (1991) created a computational model in which test ontogeny resulted from pressures and loads exerted from different directions on the test. The model predicted test shape on the basis of geometric and mechanical properties and revealed that flat shapes converged quickly toward taller shapes.

Ellers.—Ellers (1993) created a membrane model involving pressure gradients to predict curvatures exhibited by regular echinoid tests on the basis of internal pressure (Baron 1991; Ellers and Telford 1992). The model was derived from a classic analysis of thin shells (Timoshenko 1940), which involved an algorithm that created constant-strength domes, as might be observed with liquid drops. Ellers encoded the algorithm into a computer program, which was used to determine shapes and predict associated stresses for regular echinoid tests, utilizing measured pressure gradients. Following Thompson (1917), Ellers noted that curvatures exhibited by drops correspond to curvatures exhibited by regular echinoid tests. Pressure inside a liquid drop increases with depth, because the internal liquid is characterized by density that is greater than is the density characterizing the external medium. Using the computational model, Ellers was able to predict successfully curvatures for some regular echinoid tests.

Zachos.—To describe plate tessellation patterns, Zachos (2009a,b) created a three-dimensional echinoid model. Echinoid test plates were represented by Delaunay triangulation over a three-dimensional spherical coordinate system

and derived from affine deformations (Zachos 2006, 2007a,b, 2009a,b). Tests were constructed by using regular closed tiles mapped onto spherical surfaces (Zachos 2009a,b), and plates were represented by Voronoi diagrams (Aste and Weaire 2000; Zachos 2009a,b). Plate growth and migration toward the peristome during growth were calculated along geodesics (great circles), and all plate perimeter and area calculations were performed over corresponding spherical patches (Zachos 2009a,b). Plate growth was modeled by using morphogen gradient functions describing nutrient diffusions, growth factor inductions, and lateral inhibitions (Zachos 2009a,b).

Abou Chakra and Stone.—By implementing the analogy with which soap bubbles interact in close-packing formation (Thompson 1917; Raup 1968) into a computational model, Abou Chakra and Stone (2008, 2011; Abou Chakra 2010) were able to explain plate patterns and plate shapes. They applied the analogy to four biological processes that are essential in describing echinoid test ontogeny: plate addition, plate growth, plate gapping, and plate interaction (previously described as ''shifting'' in Abou Chakra and Stone 2008). The computational model is governed by mathematical principles, wherein close-packing configurations are considered in two dimensions according to Descartes circle theorem, and physical principles, wherein soap-bubble interactions are predicted using Plateau's Laws (Boys 1958; Coxeter 1969; Isenberg 1978; Aste 1996; Langarias et al. 2002).

Phylogenetic Systematic Analysis

We conducted a cladistic analysis on the aforementioned echinoid test models, by stating (i.e., identifying and prescribing) characters and defining character states. Provided that ''cross-lineage borrowing'' (Stone 1996) occurred infrequently, such a parsimony-based analysis may be applied appropriately to produce a cladogram and, thereby, interpret the history for models in this field. In fact, because parsimony is a scientific criterion independent from the criteria associated with how the echinoid models were conceptualized, were cross-lineage borrowing

	Dynamic	Mechanistic	Computational	3-D graphical	Corona Shape	Interambulacrum	Ambulacrum	Apical System	Peristome	Visceral Growth	Plate Addition	Plate Growth	Plate Gapping	Plate Interaction
Thompson 1917	1	0	0	0	1	0	0	0	0	1	0	0	0	0
Moss & Meehan 1968	1	0	0	0	1	0	0	1	1	1	0	0	0	0
Raup 1968	1	0	1	0	0	1	0	0	0	0	1	1	0	1
Seilacher 1979	1	0	0	0	1	1	1	0	0	1	0	1	0	0
Telford 1985, 1994	1	0	1	1	0	0	0	0	0	0	1	1	0	0
Baron 1990, 1991	1	0	1	0	1	0	0	0	0	1	0	1	0	0
Ellers 1993	1	0	1	0	1	0	0	0	0	1	0	0	0	0
Zachos 2006-2010	1	1	1	1	1	1	1	0	0	1	0	1	0	0
Abou Chakra & Stone 2008-2011	1	0	1	0	0	1	0	1	0	0	1	1	1	1

FIGURE 2. Matrix containing names for the nine echinoid test models and 14 character statements used in the analysis.

infrequent, its occurrence actually would be identifiable as homoplasous character states (i.e., if transferred or independently derived ideas occurred infrequently, then these would be exposed as parallelisms or convergences [Stone 1996]).

For character statements we used modeling approaches (dynamic and mechanistic), technical aspects (e.g., computational and 3-D graphical), structural components (corona shape, interambulacrum, ambulacrum, apical system, and peristome), and ontogenic processes (visceral growth, plate addition, plate growth, plate gapping, and plate interaction (see ''Morphological Models'' and ''Echinoid Tests,'' above, for descriptions); and we defined character states by scoring 0 for absence and 1 for presence (Fig. 2). We analyzed the data with the computer program Hennig86 (Farris 1988), designating as the outgroup the model proposed by Thompson (1917) and invoking the implicit enumeration command (ie*). This command guaranteed that all most-parsimonious cladograms were found. We obtained two cladograms, each with length 18 steps, consistency index = 72%, and retention index = 70% (Fig. 3). Using the nelsen command, we generated a consensus cladogram (Fig. 4), which was identical to one of the cladograms we had obtained (Fig. 3B).

Biostratigraphic Representation

We contextualize the consensus cladogram, and thereby the ''holotestoid family,'' by interpreting it as a phylogenetic tree and using a biostratigraphic metaphor to ground it. We use distance (in time, according to publication) to provide dates for events (Fig. 4). This allows us to identify different perspectives to ''holotestoidology'' (echinoid test modeling).

The base stratum contains the first model, proposed by Thompson (1917), which initiated a dynamic trend that persists to today (i.e., in Thompson's case, involving physical principles to explain corona shapes with reference to internal pressures). In that stratum and the subsequent four strata, force may be identified as a common physical principle that served as the basis on which echinoid test models originated. We recognize in each stratum one force: pulling (Thompson 1917), expansive (Moss and Meehan 1968), internal (Ellers 1993), or innate (Baron 1990, 1991). Pulling forces result from gravitational effects on tests; expansive forces are exerted from within by viscera growing outward; internal forces are generated by coelomic pressures displaced over areas; and innate forces are realized as correlated growth among tests (e.g., height-to-diameter ratios).
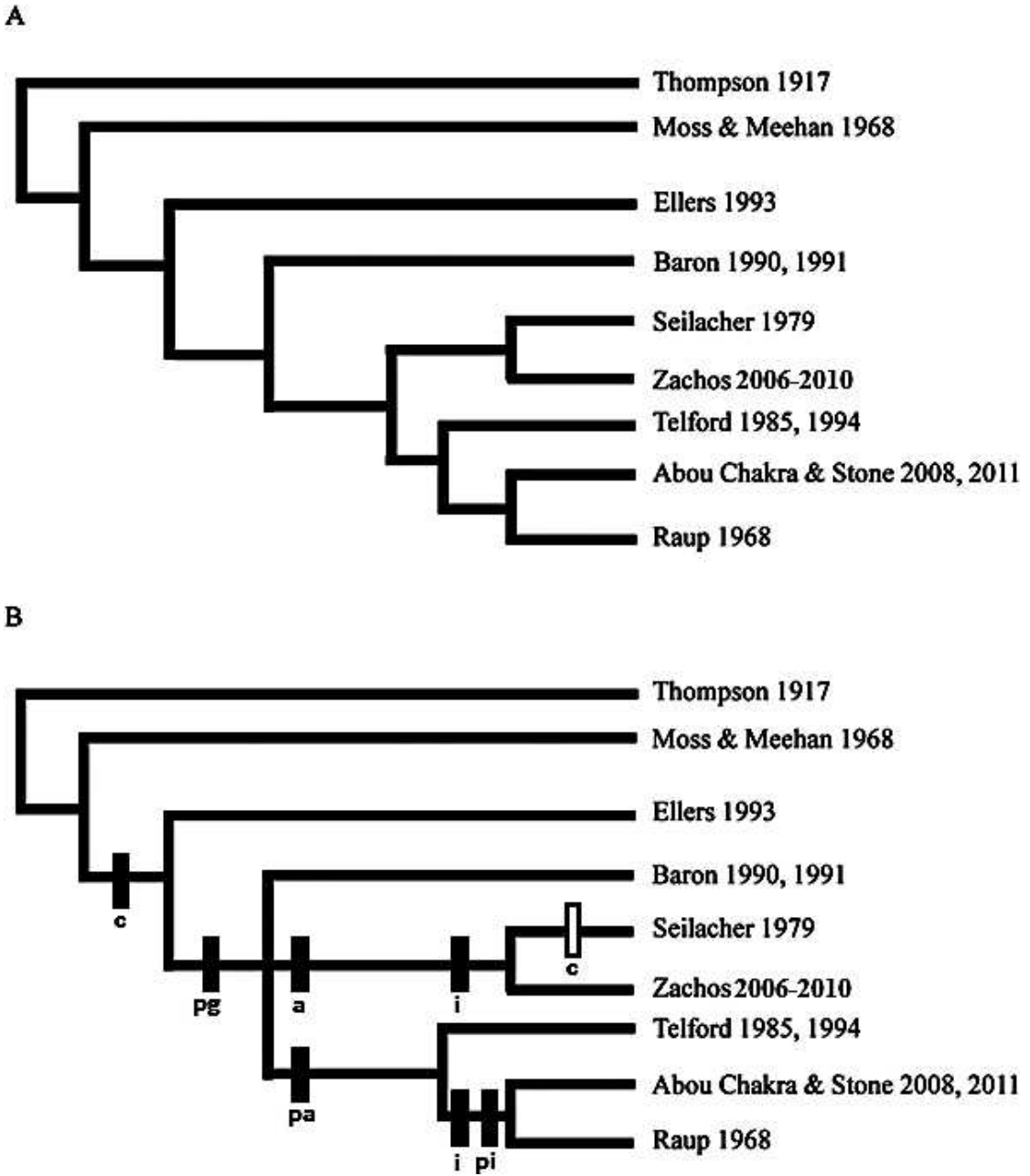
A

B

FIGURE 3. Cladograms resulting from cladistic analysis on data in matrix presented in Figure 2, among which B constitutes the consensus cladogram (only synapomorphic character states are presented. c, computational; pg, plate gapping; a, ambulacrum; i, interambulacrum; pa, plate addition; pi, plate interaction. Presence is indicated with black-filled bars; absence is represented with white-filled bar).

Lying atop those are echinoid test models in which morphology is explained by considering interaction between interambulacral and ambulacral columns as primary. We dub this clade as ''Column-Driven'' (Seilacher 1979; Zachos 2006, 2007a,b, 2009a,b). The most recent stratum contains echinoid test models in which plate ontogeny is primary; we christen this clade as ''Plate-Driven'' (Raup 1968; Telford 1985, 1994; Abou Chakra and Stone 2008, 2011).

Utility in Applying a Biostratigraphic Metaphor.—Cladograms usually are considered as
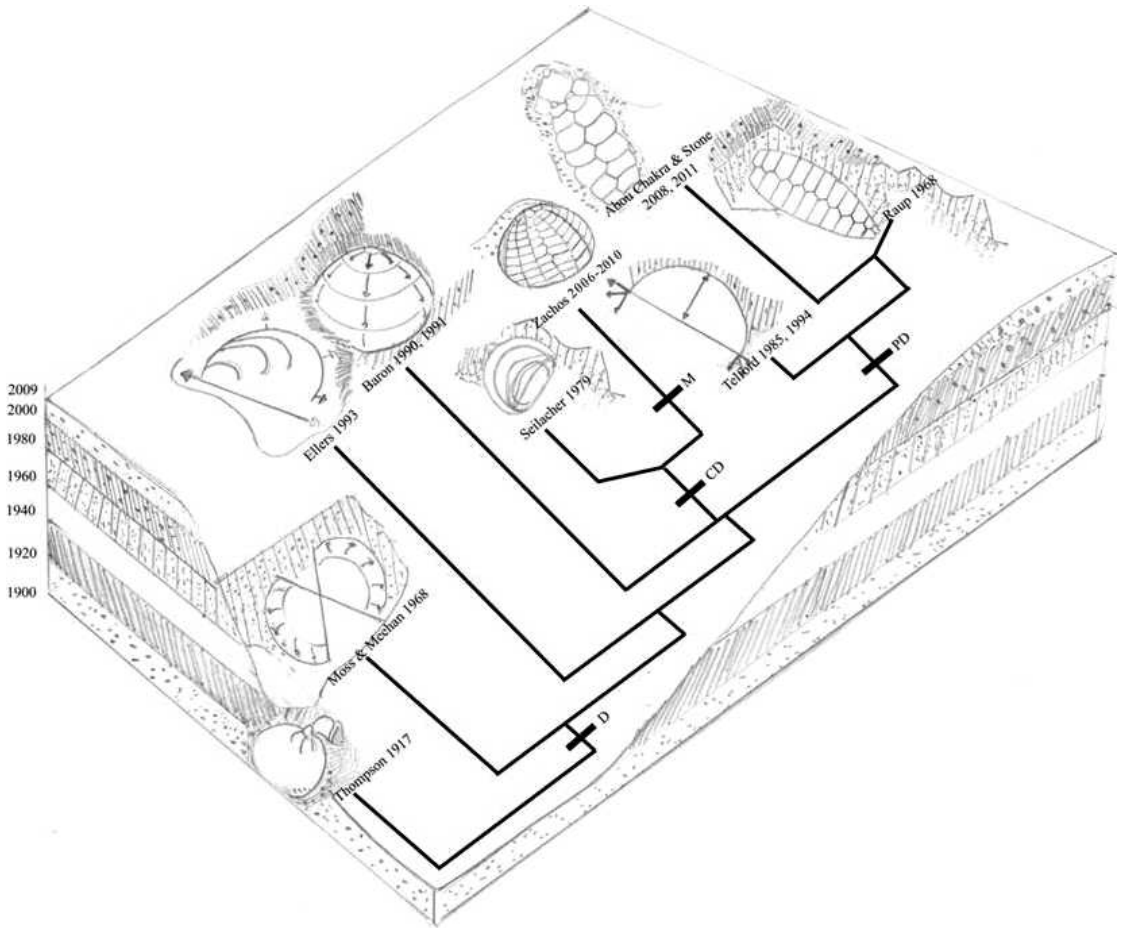
FIGURE 4. An illustration depicting the biostratigraphic metaphor: the phylogenetic tree for echinoid test models with the model species embedded in strata. Some key character states that define clades are shown: D represents dynamic approach, CD represents column-driven perspectives (ambulacrum and interambulacrum processes), PD represents plate-driven perspectives (plate addition process), and M represents mechanistic approach.

two-dimensional branching diagrams and are interpreted to represent the phylogenetic relationships among species (or other organism groups) for which actual dates of origin are unknown. Dates for events like speciation may be estimated with reference to fossil specimens. In a similar manner but with greater acuity, publications can provide origin dates for model species. And, when model species with very different origin dates are hypothesized as being related closely to one another, one may infer that similar conceptual perspectives were adopted by the respective theoretical morphologists.

The Column-Driven and Plate-Driven ''genera'' reveal this inferential utility in applying a biostratigraphic metaphor. Situat-

ing the consensus cladogram for echinoid models in a biostratigraphic context forced some internodes to contort to accommodate publication dates; consequently, the phylogenetic tree has warped twigs in those regions. This warping indicates that, in developing their echinoid test models, the authors in each genus found themselves adapting to similar ''theoretical morphology environments'' decades apart in time.

In addition to assisting us in identifying conceptual perspectives adapted to different theoretical morphology environments (e.g., column-driven or plate-driven), applying the biostratigraphic metaphor forced us to consider, attempt to differentiate between, and formulate hypotheses about ontogenesis (i.e.,

change within an individual) and anagenesis (i.e., change within a species) (e.g., Stone 1996: p. 926, ''Addendum''), when considering some models. For instance, the computational model proposed by Telford (1994) may be interpreted as a later stage in conceptual development on his previous biomechanistic model (Telford 1985). Contrastingly, the dissertation published by Baron (1990), the abstracts published by Zachos (2006, 2007a,b), and the initial model described by Abou Chakra and Stone (2008) may be interpreted as trace fossils, incomplete specimens whose component parts (e.g., morphogenetic concepts and Delaunay triangulation, respectively) could be appreciated fully when complete specimens became available (Baron 1991; Zachos 2009a,b; Abou Chakra 2010; Abou Chakra and Stone 2011).

Prospectus

Reviews generally provide comprehensive summaries for fields. This review additionally presents a unique perspective. We achieve this by combining a phylogenetic systematic analysis, to define trends, with a biostratigraphic metaphor, to explicitly identify those trends within theoretical morphology environments. This combination provides conceptual information about each model species, which can be used to develop novel models.

We aim to inspire other researchers to identify specific traits that might characterize new model species, ones that that would ''achieve maximum fitness'' in the current theoretical morphology environment and be suited best to explain macroevolutionary patterns. Such new model species would involve traits that capture biological reality and translate that reality, directly or indirectly, into algorithms. For instances, such traits would include a dynamic approach, like that in Thompson 1917 (D in Fig. 4), mechanistic approach (Zachos 2006, 2007a,b, 2009a,b) (M in Fig. 4), column-driven processes (Seilacher 1979; Zachos 2006, 2007a,b, 2009a,b) (CD in Fig. 4), or plate-driven processes (Raup 1968; Telford 1985, 1994; Abou Chakra and Stone 2008, 2011) (PD in Fig. 4).

We also aim to inspire researchers to utilize model species to explain specific macroevo-

lutionary patterns. One specific macroevolutionary pattern that has defied explanation involves the morphological disparity observed among echinoid tests. For example, although sea urchin (regular echinoid) and sand dollar (irregular echinoid) tests involve the same ontogenic processes and structural elements and even exhibit similar morphologies as imagos (i.e., ''imagines'' in Hyman 1955), as adults, they exhibit disparate test morphologies: sea urchins generally have high and oblate spheroid tests, whereas sand dollars generally have low and flattened tests (Fig. 1D,E).

An echinoid model that can be used to explain this macroevolutionary pattern has yet to originate.

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