Evolving Form and Function: Fossils and Development

Proceedings of a symposium honoring
Adolf Seilacher for his contributions to paleontology,
in celebration of his 80th birthday

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Seilacher on the Science of Form and Function

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Abstract
Adolf Seilacher’s major contribution to our understanding of the evolution of morphology has been to emphasize that function is an important, but far from complete, explanation of organic form. Recognizing the influence of phylogeny and architecture in addition to adaptation, Seilacher formalized this realization in 1970 as “Konstruktions–Morphologie” (constructional morphology). This “triangular” approach was very influential at a time when there was little interest in constraints on the evolution of form. In 1990, 20 years on, Seilacher expanded the triangle to include an environmental dimension; although this cannot be measured directly, it is important conceptually. He renamed the investigation of form “morphodynamics.” Seilacher highlighted the significant role of fabricational noise, including self-organization, intercalational hierarchies and morphogenetic countdowns, in determining morphology. He applied the methods of constructional morphology to a range of organisms, from vendobionts to barnacles, clams to crinoids. Seilacher’s results are illuminated by his unique explanatory terminology and the iconography of his line drawings.

Keywords
Adolf Seilacher, constructional morphology, morphodynamics, bivalve mollusc, Ediacara.

Introduction

Adolf Seilacher’s most important contribution to the science of form and function has been to show how factors other than adaptation influence the morphology of organisms. (His equally important contributions to our understanding of exceptionally preserved fossil deposits [Lagerstätten] and trace fossils fall mainly outside the subject of this symposium.) Seilacher formalized his approach to form in a four-page prospectus, published in Lethaia in 1970, that heralded a research program in Germany entitled “Konstruktions–Morphologie,” or constructional morphology. The approach was illustrated by a triangle (Figure 1), whose corners represent the influence of phylogeny and architecture as well as adaptation. Different terms for these corners have been used in different descriptions of the approach—historical, morphogenetic and functional, for example—but the meanings are the same. It is important to note that, in emphasizing historical and morphogenetic factors, Seilacher was in no sense rejecting the importance of adaptation. The principles of constructional morphology formulated by Seilacher have been applied...
successfully to entire organisms as well as to functional units within them (Schmidt-Kittler and Vogel 1991). The approach envisions the organism or feature as one point in a dynamic process (like a single frame from a movie); its morphology provides evidence of the influence of different factors during its evolution.

The phylogenetic or historical corner of the triangle (see Figure 1) represents the “bauplan,” or diagnostic morphology, of a major group. This inherited aspect of morphology clearly limits responses to natural selection. The accretionary growth of molluscs, for example, incorporates the morphology of the juvenile into the adult, and both must be functionally compatible. Arthropods, on the other hand, grow by molting and the larva may metamorphose into an adult with a completely different lifestyle (such as the free swimming cyprid larva, which becomes a sessile goose barnacle).

The fabricational or architectural corner has been a particular focus in Seilacher’s research on form. It identifies the influence of available materials and self-organizing processes. These factors are usually expressed in the growth of the organism. The most familiar example is the computer simulation of the logarithmic spiral in the classic papers by Raup (for example, Raup 1966). Important evidence for the underlying principles are provided by repair structures and fabricational errors. The emphasis is on the observation that morphology is a response to factors other than adaptation.

The functional corner of the triangle acknowledges the insights provided by Rudwick’s (1961) paradigm method for analyzing function. The role of adaptation is often difficult to identify as the form of many structures reflects natural selection for several different purposes (crustacean appendages, for example, are often used in feeding, locomotion and respiration). The paradigm method has been applied in its strictest sense to unusual structures that cannot be interpreted through a straightforward comparison (Hickman 1988). In such cases alternative func-

Figure 1. The original Konstruktions–Morphologie triangle (after Seilacher 1970).
tions can be identified to provide a basis for paradigms that can be compared with the structure under consideration.

Rudwick's (1961, 1964) paradigm method provided a robust procedure for analyzing function in fossils (Gould 1970), but it obscured other important influences on the evolution of form. Gould and Lewontin (1979) criticized the adaptationist programme and emphasized the role of phylogeny and architecture in determining form (they used the spandrels in the dome of St. Mark's Cathedral in Venice as an example of a morphological feature without any structural function). Their paper advocated a pluralistic approach to understanding form rather than interpreting the individual attributes of an organism in isolation. Gould and Lewontin (1979:595) acknowledged the emphasis placed on architectural constraints by Seilacher, "whose work deserves far more attention than it has received." They highlighted the example of divaricate patterns (structures that diverge from a point and run obliquely to the growth direction) in the shells of molluscs and brachiopods (Figure 3). As Seilacher (1972) pointed out, the divaricate pattern is functional only in a small proportion of cases: as burrowing sculpture, mimetic color, and to allow light to penetrate to endosymbiotic algae. Seilacher used divaricate patterns as a major example in formalizing the concept of fabricational noise, that is, morphological features that are the result of architectural constraints rather than functional adaptation, but can be subject to selection (Seilacher 1973). He showed how these patterns lend themselves to co-option as burrowing sculptures. In emphasizing that morphology is a response to factors other than adaptation, Seilacher's influence was profound.

Other authors identified additional factors that influence form: Raup (1972) added chance and ecophenotypic effects in his review of the analysis of morphology; Hickman (1980) added mechanical, ecological, programmatic, maturational and degenerative factors in her consideration of gastropod radulae. Criteria such as these, however, can be subsumed within the major factors that defined Seilacher's (1970) original triangle (see Thomas 1979).
The original constructional morphology approach was independent of the postulate of evolutionary change, but certainly not incompatible with it (Reif and others 1985). Seilacher (1984) regarded constructional morphology as a method of research rather than a theoretical framework, but acknowledged that accumulated results might lead to the identification of wider patterns. Twenty years after the original formulation Seilacher (1991) expanded the triangle to a tetrahedron to include an environmental dimension (Figure 2). At the same time he named the analysis of form “morphodynamics” to emphasize that morphology represents the result of evolution, and therefore encapsulates evidence for the factors that influenced change in form through time (Seilacher 1991). Seilacher (pers. comm. in 2004) argues, however, that “as environmental parameters cannot be directly measured in fossil examples, this aspect is important only in a conceptual sense.”

Since 1970 Seilacher has applied the concept of constructional morphology to a range of examples across the taxonomic spectrum. He regards fossil invertebrate skeletons as “a treasure-house of evolutionary experimentation ready for morphodynamic analysis” (pers. comm. in 2004). A major achievement of Seilacher’s approach to the analysis of form has been the identification of features that transcend specific morphologies and taxa—self-organizational patterns, intercalational hierarchies, and terminal and iterative countdowns—and the demonstration that they are mainly fabricational noise, and not primarily a response to function.

Self-organization

One of the most striking examples of self-organization is the pneu, a fluid- or gas-filled chamber. No Seilacher course on morphodynamics is complete without the demonstration of a water-filled balloon. Ellipsoids and domes form automatically whenever a tensional membrane encloses a denser or pressurized shape (Seilacher 1991). A water-filled balloon adopts a shape similar to that of many regular echinoids, and Seilacher argued that tensional forces are translated into an echinoid test that is “automatically optimized” (1991:257) to distribute compressional forces within the rigid wall.

Philippi and Nachtigall (1996) used finite element analysis to show that the shape of an echinoid is a response to complex factors, particularly the mechanical activity of the ambulacral tube feet (see Smith 2005). The pneu hypothesis of test shape is doubtless an oversimplification, but that is precisely the point—it provides an explanation of the origin of the shape. The vaulted
Figure 4. Intercalational hierarchies. Intercalating ribs and spines in the gastropod *Murex pecten*, and the bivalves *Neithea regularis*, *Spondylus sinensis* and *S. mirabilis*. The arrangement of spines is hierarchical. After Seilacher 1991, fig. 11. Used with kind permission of Springer Science and Business Media.
domes of echinoid tests, and the configuration of the plates, may reflect the pneu principle even though the shape is modified by differential growth and other factors (Seilacher 1991:258). Seilacher’s (1979) analysis of the constructional morphology of sand dollars showed how the pneu shape can be modified for burrowing and sieve feeding with diverse novel features, including allometric plate growth and tethering of the upper and lower surfaces with pillars of stereom. Seilacher used the principle of a marginal pneu, likewise modified by tethering, to explain the shapes of coral polyps (circular in isolation, hexagonal in contact) and the shape of the margins of bivalves, which grow by accretion (see Seilacher 1991).

Zebra patterns (Figure 3) provide a second example of self-organization. Expressed as lines or spots, in color or sculpture, they are characterized by bilateral asymmetry and occur on many animals, not only as the stripes on the eponymous zebra, but in our own fingerprints. Some of Seilacher’s earliest work (in the 1940s) identified zebra patterns in the ridges on the surface of the teeth of hybodont sharks (see Seilacher 1973). “Normal” zebra patterns occur on nongrowing
structures (egg shells, adult cowries) or on expanding skins (fingerprints, mammal skins) (Seilacher and Gunji 1993: 240). The divaricate patterns on bivalves and other shells are the result of self-organized zebra patterns combined with marginal growth (Seilacher 1991).

Seilacher (1991) considered self-organizing patterns to have begun through a physical process. He envisaged them being brought under genetic control and modified by selection to fulfil a particular function. The evidence for the conflict between self-organization and genetic control is seen in occasional morphological flaws “in which the autonomy of the mechanism expresses itself beyond the adaptational straight-jacket” (1991: 265). Seilacher has exploited these “mistakes” to identify the nature of the underlying control. He provided an elegant example in a population of Strigilla pisiformis from Miami (Seilacher 1984) where the underlying divaricate pattern, which has been modified to provide a burrowing sculpture, is revealed by individuals that have suffered damage at the shell margin.

Intercalational Hierarchies

Seilacher noted that the cyclic insertion of elements during growth (intercalation) generates a hierarchy (Seilacher 1991). This is readily seen in crinoid stems that increase their length by the cyclic introduction of internodals. Similar patterns occur in the ribs of various molluscs and the spines that they bear (Figure 4). Seilacher showed how such intercalation of ribs produces the extraordinary arrangement of spines in the gastropod Murex pectin, where rank in the hierarchy determines both the size and orientation of the spines. The spines enclose and protect the feeding snail (Paul 1981). Seilacher (1991) argued that ammonite sutures incorporate elements of an intercalational hierarchy in the insertion of tie points where the body membrane was attached to the shell. The shape of the suture, however, was a response to pneu-like bulging between the tie points.

Morphogenetic Countdown

Seilacher used the term “morphogenetic countdown” to describe a change in the pattern of growth in a spiral shell as the adult morphology is reached (Seilacher and Gunji 1993). The concept is illustrated by coloration in Nautilus, where color bands disappear on the ventral side of the shell in anticipation of the termination of growth, and the shell becomes countershaded as the final aperture forms. Seilacher argued that this change in “terminal” morphology does not imply a change in lifestyle, nor a loss of fitness (Seilacher and Gunji 1993).

Seilacher and Gunji (1993) used the concept of morphogenetic countdown to analyze heteromorphs in gastropods, ammonites and brachiopods. Countdowns are very common in gastropods, beginning before the growth of the final aperture and improving fitness only when complete. Countdowns extend beyond the self-organization of the logarithmic spiral; in Seilacher’s words they “require a fixed program that must be almost verbally written down in the genome” (Seilacher and Gunji 1993: 245). Countdowns may occur iteratively, a phenomenon particularly well illustrated by muricid gastropods, whose varix spines reflect sequences of morphogenetic commands superimposed on the underlying program (Seilacher and Gunji 1993; see Figure 4). Here is a phenomenon that has yet to be explained in terms of evolutionary development.

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Figure 6. Soft-bottom oysters. Adaptational strategies in oysters that have become soft-bottom dwellers. After Seilacher 1984. Used with permission of The Palaeontological Association.
pressure with the saddle muscles would allow the ammonite to rise in the water column again. The advantage is energy conservation—moving through the water is essentially passive.

This interpretation of heteromorph ammonites is a classic example of the application of morphodynamics in place of functional homology (in this case with Nautilus). Seilacher advises that we should not be blinkered by comparisons between fossils and their nearest living relatives. The Nautilus model argues for neutral buoyancy and active swimming, difficult to reconcile with some of the unusual attributes of heteromorph ammonites. Seilacher argued that, while the nautiloid septum corresponds to a pneum, the ammonite septum behaves like an elastic membrane spread in a frame (Seilacher and LaBarbera 1995). As Seilacher and LaBarbera (1995) pointed out, a difficulty with the Cartesian diver model is that calcification of the membrane in the growing ammonite without distortion would seem to require a period during which there was no change in the depth at which the animal was living. The Cartesian diver model may apply only to the later stages of ammonite evolution.

Constructional Morphology of Bivalve Molluscs

Some of Seilacher’s most compelling applications of constructional morphology have been to bivalve molluscs. Here he took advantage of the signal provided by convergent morphologies to explore the constraints imposed on the radiation of bivalves in soft-bottom settings (Seilacher 1984, 2005b). He considered the function of the elastic ligament that opens the shell, and the role of burrowing sculptures, particularly those resulting from divaricate patterns. The recolonization of soft substrates from sessile attached modes of life is particularly interesting because these bivalves have lost the foot (which was replaced by the byssus, or cementation for attachment to hard substrates) and have no obvious method of anchoring themselves. The colonization of soft substrates occurred many times and allows a comparison of convergent morphologies. The initial stage involves larval attachment to tiny islands of hard-part substrate (shell fragments on the sediment surface) and miniaturization of the adult. The major strategy adopted is stabilization of the body by shape, weight and size.

In the case of the cemented oysters the growth program had been “derailed” (Seilacher 1984:214) to allow them to mimic the substrate, and this may have promoted modification of the shell morphology in derivatives that returned to soft bottoms. They gave rise to a variety of heavyweight recliners and lightweight mud stickers (Figure 6). Byssate, as opposed to cemented forms, show convergent strategies, but the shells do not become as heavily thickened because the byssus provides an additional source of stability. Rather than resting on one valve, byssate forms often evolved into edgewise recliners. Horn-shaped growth, as in Gryphaea and rudists such as Hippurites, allows the shell to be righted passively if it is toppled; erosion creates an upcurrent depression into which the shell rotates.

Seilacher (1998) extended his investigation of bivalves to consider the bizarre rudists of the Cretaceous, where the ligament is reduced or absent (he suggested that the shell was opened by a unique system of diductor muscles). The loss of the ligament allowed the two valves of rudists to grow independently: the lower one straight, the upper reduced and anchored as a lid. The presence of diverticles, particularly in the upper valve, indicates that rudists harbored photosymbiotic algae. Rudists, in Seilacher’s view, went beyond “liberation from traditional morphogenetic constraints” to “deviant lifestyles” (1998:435).

The application of constructional morphology to make comparisons within larger groups, as in Seilacher’s (1984) study of soft-bottom dwelling bivalves and Seilacher and Hauff’s (2004) on pelagic crinoids, helps to elucidate evolutionary pathways. The approach can also be applied to a particular clade, as in Thomas’s (1978a, 1978b) analysis of arcoid bivalves, which considered the limits on morphological evolution. Phylogenetic constraints on the evolution of form in arcoid bivalves include: their possession of a spirally coiled calcareous exoskeleton, gills and a muscular foot (as molluscs); their bilateral symmetry, elastic ligament, adductor muscles and
Figure 7. Zebra patterns in a micritic crust on a slab of Upper Jurassic limestone from Westerstetten, Ulm, Germany (× 8.75). After Seilacher 1997. Used with permission.
an attachment organ (as bivalves); and their shell microarchitecture, with serial ligament and hinge structures (which are specific to arcoids). Fabricational constraints include accretionary growth in a spiral, and the simple composition and growth pattern of the ligament. The ligament is weak, and is unable to brace the shell firmly against the substrate during burrowing. The simple gill provides an inefficient pump, which may explain why the arcoids did not develop siphons. Thus a combination of phylogenetic and fabricational constraints explains why the radiation of arcoids yielded only generalists, either shallow burrowers or byssate nestlers.

Epibionts

Seilacher pioneered the use of epizoans as important evidence in the interpretation of form and function. He used observations of the standard orientation of a range of epizoan taxa to interpret the swimming orientation of the ammonite Buchiceras, which they encrusted (Seilacher 1960). This study confirmed that the ammonite lived in the water column, that the shell was not covered by soft parts, and that the adult stage lasted for years. More importantly, Seilacher pointed out that the method could become “a key to the still controversial ecology of uncoiled and aberrant types” (1960:193). For example, he used traces of barnacle borings in the guard to confirm the swimming orientation of belemnites (Seilacher 1968). Most recently he showed how some species of barnacle managed to settle on whales (Seilacher 2005a).

Seilacher has also considered the symbiotic relationship between various epizoans and their hermit crab hosts. Here the morphology of the encruster is controlled by external forces rather than morphogenetic information (Seilacher 1991, 2005b). The epizoan grows to maintain its position adjacent to the food supply and to avoid becoming immersed in the substrate on which the crab lives. Its form is determined by the activities of the hermit crab.

Ediacaran Organisms

One of the most striking examples of Seilacher’s application of the constructional morphology approach was to the remarkable Ediacaran fossils of the late Precambrian (see Gehling and others 2005), at a time when conventional wisdom held that they all represent metazoans, the ancestors of modern organisms. Seilacher (1985) was impressed by the anomaly of the widespread occurrence of a range of soft-bodied organisms preserved (in some cases) in relatively coarse sediment. This taphonomic anomaly has been solved, at least in part, by Gehling’s (1999) death mask hypothesis, which explains the preservation of Ediacaran fossils by bacterial precipitation of iron minerals in association with the buried carcasses (Gehling and others 2005). Seilacher explained the rarity of this type of preservation in the Phanerozoic as a result of the diversification of bioturbators (the shift of the seabed from a “matground” to a “mixground”) (Seilacher and Pfüger 1994; Seilacher 1999).

More importantly, Seilacher (1985) noted that many of the Ediacaran organisms shared a common architecture. He deduced that they were constructed as a series of chambers or pneus, a structure akin to quilting, and argued that they could not be interpreted as conventional metazoans. “The main function of this provocative hypothesis is to stimulate research in Precambrian palaeontology and to free it from taxonomic preconceptions” (Seilacher 1985:48). This illustrates one of the major strengths of Seilacher’s approach, his ability to see beyond the organism to its underlying organization. In the absence of any phylogenetic constraint, Seilacher (1989) was able to consider the form of the Ediacaran organisms on purely constructional principles (that is, as architecture moderated by functional design). He started with the premise that they “represent an exotic principle of organismic construction” (Seilacher 1989:230). He regarded Dickinsonia, for example, as a quilted pneu with a thin and flexible outer skin, but with somewhat more rigid internal struts (but see Gehling and others 2005). Seilacher’s “pneu” interpretation suggested that the morphology was likely to be a response to a need to maximize surface area for the uptake of nutrients, and for respiration and excretion. He also considered that these Ediacaran organisms,
which he termed Vendobionta (Seilacher 1992), may have harbored bacterial symbionts (Seilacher 1989). Having deduced the architecture of the vendobionts, Seilacher (1989) pointed out that there are no living models on which to base an interpretation of function. He recognized the possibility of radial, unipolar and bipolar growth and, most interestingly, the fractal organization of some forms. He conceded that his interpretation of the outer skin and internal organization was, of necessity, speculative, but constrained by observations on the nature of their preservation. Following research on the specimens found at Mistaken Point in Newfoundland, Seilacher (1992) expanded his analysis of Ediacaran fossils to interpret the various lifestyles of vendobionts as sediment stickers, flat recliners or erect elevators (once again constraining his interpretation of the function of these organisms with observations on the nature of their preservation). The interpretation of Ediacaran life developed another novel twist when Seilacher suggested that many of the vendobionts represent giant protists (Seilacher and others 2003), an idea that he had first put forward in 1992 (Seilacher 1992). Seilacher interpreted those Ediacaran forms that lived within the microbial mats as xenophyophores (a group of giant marine rhizopodan protists with an agglutinated wall, which today are restricted to abyssal depths), and considered many of the more familiar vendobionts to be representatives of an extinct class of giant rhizopods (Seilacher and others 2003). This extended interpretation does not alter Seilacher’s analysis of the form of Ediacaran organisms; it simply attempts to make sense of their affinities.

Nonbiological Analogies

Seilacher has a remarkable ability to see pattern and extract lessons from abiotic phenomena such as balloons, architectural designs, soap bubbles, convection cells in confined fluids and frictional ridges on skis. The experiments that he carried out on candle wax shells with Christian Klug are a classic example of this (Seilacher and Klug 1993; Seilacher 1994). Such “shells” are produced when molten candle wax flowing into water solidifies. The morphology of the shells is determined by the temperature of the water: in cold water the shells are narrow and highly convex with prominent growth lines; in warmer water they become wider and flatter and the growth lines become fainter. Seilacher drew a lesson from the similarities to the shells of bivalve molluscs: “regular shell geometries result from relatively simple sets of parameters and processes” (Seilacher 1994:274), and growth lines are “an essential element of accretionary shell growth” (Seilacher and Gunji 1993:239).

Seilacher’s fascination with form led directly to the assembly of his, now internationally travelled, exhibition *Fossil Art*, funded from his 1992 Crafoord Prize. The exhibition presented some 34 large slabs with spectacular examples of many of the phenomena that Seilacher has made the subject of scientific study, from Ediacaran organisms to trace fossils, as well as a small number of inorganic patterns. These last include sedimentary structures such as mud cracks and ripple marks, but also a swirling zebra pattern generated by precipitation on a limestone block from the Jurassic of Germany (Figure 7). Patterns in nature can be as visually arresting as they are scientifically challenging. As Seilacher (1997:60) said, "the limits of ‘art’ are not clearly defined.”

Conclusion

The influence of Seilacher’s research on form and function has been fundamental: several publications have been devoted to constructional morphology (Schmidt-Kittler and Vogel 1991), and the approach has been applied to diverse organisms, stimulating an enormous literature. Seilacher’s ideas are often radical and several, including his interpretations of the Ediacaran biota, became widely known through the force of his presentations and the power of his personality long before being published in detail (Seilacher 1989). Some encountered resistance from reviewers and editors and took some time to appear in the mainstream literature.
The long-term influence of Seilacher’s ideas is guaranteed, however, not only because of their scientific content, but also because of his singular explanatory terminology—constructional morphology, morphodynamics, zebra pattern, iterative countdown, sediment sticker, vendobiont, Fossil Lagerstätten—and his iconic drawing style.

Acknowledgments

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Literature Cited


Appendix: Publications by Adolf Seilacher


86. **Seilacher, A.** 1982. General remarks about


171. **Gehling, J. G., B. Runnegar and A. Seilacher.** 1996. Rasping markings of large


* Reports of Sonderforschungsbereich (SFB) 53, in some cases including results of other members.