ACTA PALAEONTOLOGICA POLONICA

Discussion

Vol. 38, No. 3/4, **pp.** 273–280, Warszawa, 1994

Candle wax shells, morphodynamics, and the Cambrian explosion

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What I miss most with Antoni Hoffman is the ideal discussant for trying out new and often controversial ideas: very sharp and critical, yet warm-hearted enough not to become polemic. The last time we met, I told him about our candlewax shells and their implications for the emergence of new bauplans (Seilacher & Klug 1993). Surprisingly he reacted unlike the editors of a leading science journal who had just rejected my note without asking a referee. Instead he encouraged me by saying this was the deepest thought he had ever heard from me. Thank you, Toni! So here is the story again, hopefully in a more ordered form.

Candle wax shells

The experiment. — The crucial discovery was made by our Tübingen student Christian Klug, or rather his mother. During Christmas preparations, she had placed a burning candle into a bowl of water. The bottom of the massive float that grew in the water from the molten wax (Fig. 1) resembled a real bivalve shell to the extent that even a specialist could be fooled. There was not only the familiar geometry of a spiral cone with large expansion rate; the shell also bore a hemispherical prodissoconch at the umbo and sets of growth lines mimicking daily and monthly increments.

Repeating this unsophisticated experiment under controlled conditions, C. Klug and H. Luginsland produced hundreds of such wax shells. In spite of great variability, they show a general rule: populations grown in cold water have narrow and highly vaulted geometries and bear heavy growth lines (*Gryphaea* type; Fig. 2A–C). With rising temperatures, the expansion rate increases, outlines become more circular and growth lines fainter (*Placuna* type; Fig. 2H). Eventually, as the water reaches the melting point of the wax, shells switch into the morphospace of floating oildrops that we know from a good broth.

Attempts to simulate , by the same procedure, fully coiled ammonite or gastropod shells did fail for practical reasons. The manipulations necessary (growth around a floating tooth stick; lateral shift of the wax source) invariably derailed the growth process. Minor translation (and low-degree helicoidality), however, did occur in variants in which a slight asymmetry happened to become enhanced during further growth of the float. Only patelliform cones could be produced by pouring the molten wax freely down on the water (Fig. 3A).

Some of the occasional monsters tell stories of their own. If, for instance, the initial structure consists of many clustering drops instead of a single one, the accretionary spiral coils in proportion to the enlarged radius and starts with a sharp angle – as it does in oysters with broad attachment areas (Fig. 3B). Or, when a floating dirt particle has locally indented a growth line, it takes several more increments to restore the smooth curve – just like in mollusc shells 'healing' a marginal bite mark.

Reductionistic Interpretation.— In line with our scientific tradition, we may try to identify the local controls responsible for corresponding features in the two systems:

	Wax float	**Bivalve shell**
Prodissoconch	free pneu surface of initial drop	replica of hydrostatic veliger larva
Growth lines	wax flow freezes marginally in small increments	rhythmic growth phases of mantle are frozen by biomineralization
Rounded contour	pneu surface of molten wax, guided by contour of previous margin (Markov Effect)	tension of fluid-filled periostracal margin, controlled by previous growth lines
Flat commissure	control by water table	control by margin of opposite valve
Spiral growth	flexible connection of float with candle causes tilting	flexible ligament, with tendency to expand laterally for hinge function
Helicoidality	accidental overload on one side, self-enhancing	anatomical anteroposterior differentiation
Crowding of growth lines	differential immersion decreases with size	growth rates decline with age

In this view, candle wax shells only confirm what has already been known from computer simulations: regular shell geometries result from relatively simple sets of parameters and processes, whose variability defines a certain morphospace.

But does a mere list of determining factors – however complete – do justice to the phenomenon as a whole? In an organism, individuality emerges because each shell is an integrated structure with a particular history. Why not in a physical system?

Holistic Interpretation (Morphodynamics).— In the view of Gunji et *al.* (in press), biological systems are non-programmable in principle. Not that there is no program behind; but since informations propagate and are translated by enzymes (and therefore more slowly than in physical systems), other signals or state changes can interfere during the process. As a result, the outcome can never be predicted in every detail. This means that computer simulation refers only to the basic, programmable part of a biological structure. The rest is either random or has the aspect of finality.

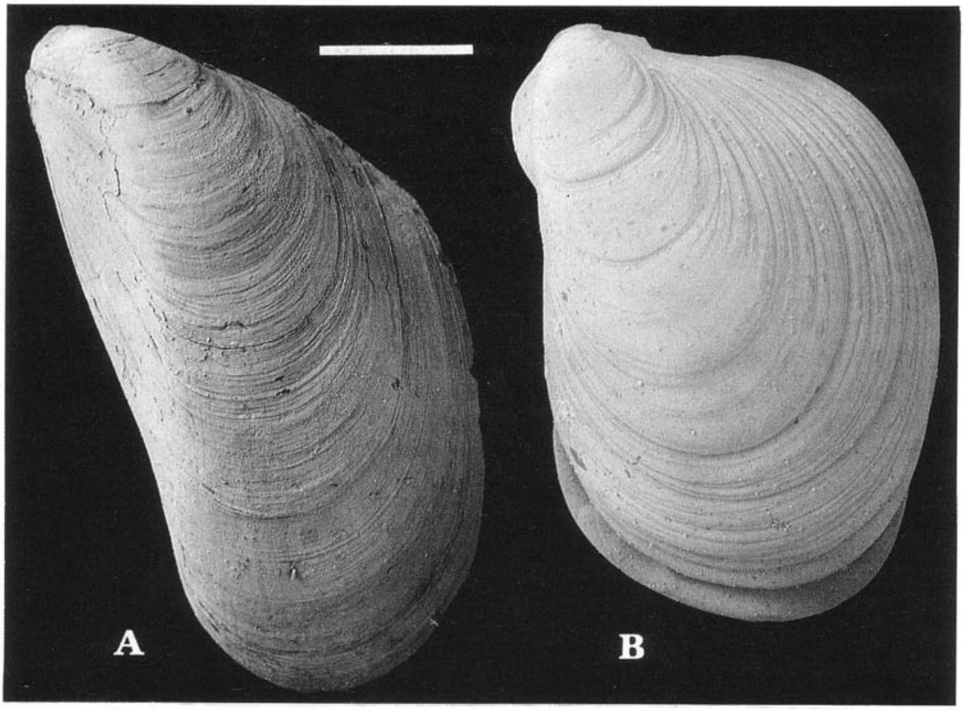

Fig. 1. The lower surface of a self-organized candlewax float (B) could be easily mistaken for the cast of a real bivalve (A), complete with prodissoconch, daily and monthly growth lines and spiral cone geometry. Scale bar – 1 cm.

Wax shells come closer to biological reality than computer simulations, because they imply unpredictability at the local level, historical (Markovian) self-reference and a finite size imposed by the dimensions of the experimental setting.

In the above list, one feature of the wax floats deserves special attention: the growth lines. In an organism, we use to relate them to fluctuations in the physiological state, whether intrinsic or environmentally imposed. But wax shells form in minutes, under constant conditions and from a continuous flow, comparable to lava flowing into the ocean. Thus the growth lines observed in either case reflect an intrinsic rhythm generated by the self-referent interaction between molten and frozen states. In such synergetic oscillations (Haken 1983), it is also a familar phenomenon that higher-order periodicities emerge on top of the lower ones.

The mantle/shell complex of a real mollusk forms a similar interactive system. During growth, biomineralization freezes the previous soft state whose shape was controlled by the mantle edge and a hydrostatic periostracum fold. At the same time, the frozen edge serves as a scaffold for the next growth ring. Since growth rings are also found in mollusc shells from the deep sea (i.e. in the absence of tidal, diurnal and seasonal forcing), rhythmic growth appears to be an intrinsic quality of biological skeletons

– which does not exclude secondary linkage with external periodicities in particular environmental settings.

This insight has consequences for sclerochronology; but more important is the message that in morphogenesis one should not even think of skeletons and soft parts in isolation, because they form the necessary partners in a synergetic system. Nobody would challenge the statement that a mollusc or brachiopod shell is the product of the mantle. But the opposite is equally true in this self-referent system: the shell produces the mantle!

The Cambrian turnover

The sudden appearance of skeletonized animal phyla at the base of the Cambrian is perhaps the greatest riddle of the biohistorical record. In reality, it presents us with a whole bundle of problems: (1) the suddenness of the evolutionary event, (2) its synchroneity, (3) the ecological turnovers combined with it.

Suddenness ('Cambrian explosion').— In the gradualistic view, animal phyla had their roots far back in the Proterozoic, but became visible in the fossil record only with the acquisition of hard skeletons (e.g. Conway Morris 1990). If one assumes, however, that the impressions of large soft-bodied organisms of the Late Precambrian ('Ediacaran Fauna') represent an extinct clade unrelated to modem animal phyla (Vendobionta hypothesis; Seilacher 1992a, b), this view looses considerable substance. On the other hand, behaviorally differentiated trace fossils tell us that small, worm-grade bilaterians with highly developed locomotory and neural systems did burrow and forage underneath microbial mats long before the Cambrian revolution.

Alternatively, the punctualistic view faces the old problem of 'hopeful monsters'; i.e. the emergence of new bauplans by a small number of serendipitous macromutations, for which known microevolutionary mechanisms fail to provide actualistic models. If, however, bauplans (like many innovations at lower taxonomic levels; Seilacher 1991) arose largely by synergetic self-organization, their relatively sudden appearance becomes more acceptable.

The synergetic view may also solve another problem. In recent years, molecular distances of DNA and its products in present-day organisms have increasingly provided us with a key to phylogenetic relationships, in addition to morphological similarities and the fossil record. According to molecular data, branching points between modem phyla appear to predate the Cambrian explosion (Bergstrom 1986); i.e. they favor a more gradualistic view. Synergetic innovation, however, may revolutionize morphological design without affecting the molecular clock. An Early Cambrian mollusc was probably close to its worm-like Precambrian ancestor in molecular terms, yet represented a fundamentally different world with regard to design and life style. Therefore, incongruence between molecular

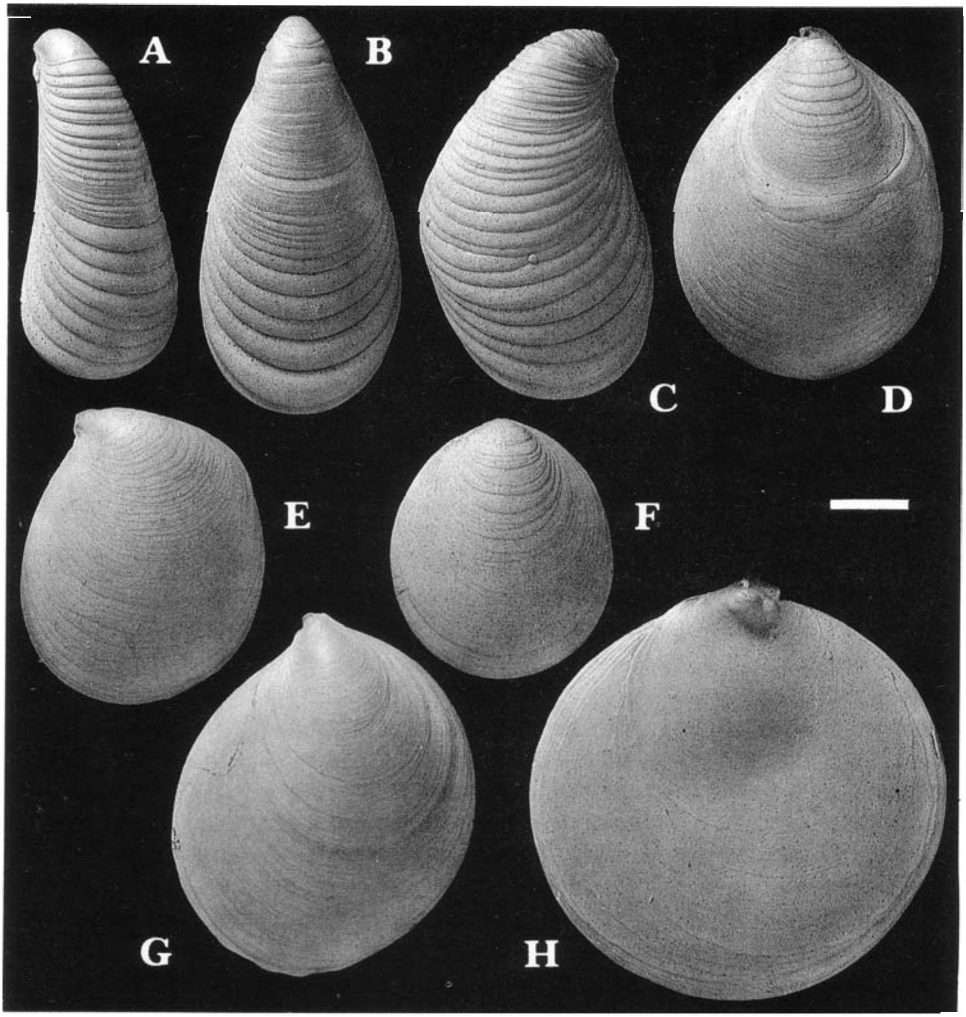

Fig. 2. Candlewax shell morphologies change consistently with water temperature. In cold water they tend to be narrow and highly convex with prominent growth lines (*Gryphaea* type: A–C). At higher temperatures, shapes get wider and flatter, while growth lines become fainter (*Placuna* type; G–H). Above the melting point, wax floats switch into the morphospace of oil drops. Scale bar – 1 cm.

and structural disparity should be expected, the first suggesting a more gradualistic, the other a punctuated mode of change.

Synchroneity of skeletonization. — Firstly , the 'big bang' view of the Cambrian revolution needs to be relativated. In geohistoric perspective, 'sudden' may still mean a million years. Also, some skeletal phyla (e.g. Bryozoa and Chordata) are as yet undocumented in the Lower Cambrian.

On the other hand, rigid animal skeletons do occur already in the Vendian; but they differ in principle from later ones. Thus, the internal sand skeletons of Psammocorallia (Seilacher 1992a), and possibly of early sponges, appear to have been held together by an organic cement that disintegrated soon after death. Also the calcareous cone-in-cone tubes of *Cloudina* are not accretionary skeletons in a morphodynamic sense. They rather resemble the tail of a rattle snake, in which instant skeletons of earlier molting stages remain attached to each other without direct self-reference – a principle that would never lead to coiled shells.

Nevertheless, the simultaneous appearance of rigid and variously mineralized skeletons of disparate designs at the base of the Cambrian remains a strange phenomenon.

Among the new constructions are not only the accretionary shells of mollusks and brachiopods. Some mollusks or annelids developed armors made up of numerous small sclerotomes that either come in a standard size and increase in number during growth; or the elements grow individually by accretion and thereby enter the morphospace of logarithmic cones. *Halkieria* (Conway Moms & Peel 1990), like modem chitons, used both principles in different sclerotomes. In contrast, arthropods molting their cuticular skeletons use mutualistic hard/soft self-reference in another manner. Instead of growth rings, a whole new cuticle replicates the rigid old layer from inside and becomes hydrostatically blown up and modified before it rigidifies itself.

In endoskeletons, intrinsic rhythmicity is less obvious. Echinoderm stereom is an intra-syncytial spicular meshwork. Yet, its morphology at microscopic and macroscopic (ossicle)levels reflects the interaction of the soft and rigid components, while the immanent rhythmicity of the fabricational process is reflected by the presence of growth rings even in tropical or deep sea species. Growth lines are even more difficult to detect in the equally intracellular spicules of sponges or protists. Still there is no reason to believe that they grow continuously.

If one includes the various biominerals used by different Cambrian animals (aragonite, calcite, Mg-calcite, phosphate, opal, etc.; Lowenstam & Weiner 1989) the disparity of the new world of skeletons becomes still more striking. It strongly suggests that Cambrian skeletonization was an event affecting different clades at the same time. Because skeletons of any kind are not simply an addition to old bauplans, but imply a new synergetic level in morphogenesis, the soft-bodied ancestors would bear little resemblance to their skeletonized offsprings and could have been of either worm or larviform grades.

External or internal triggers? — The ultimate cause for this multiclade revolution must clearly have been extrinsic. Critical changes in atmospheric and hydrospheric chemistry may have played a role. Symbiogenesis with mineralizing bacteria is another possibility (Lowenstam & Weiner 1989). But once infestation had occurred, experimentation with the new morphogenetic element, rigid skeletons, became an intrinsic, biological affair. This experimentation operated at once. In the earliest shelly faunas, mollusks are already represented by distinct classes and even orders – rather than a protomollusc archetype. Early differentiation also applies to arthropods and echinoderms. In the latter, calcichordates pose

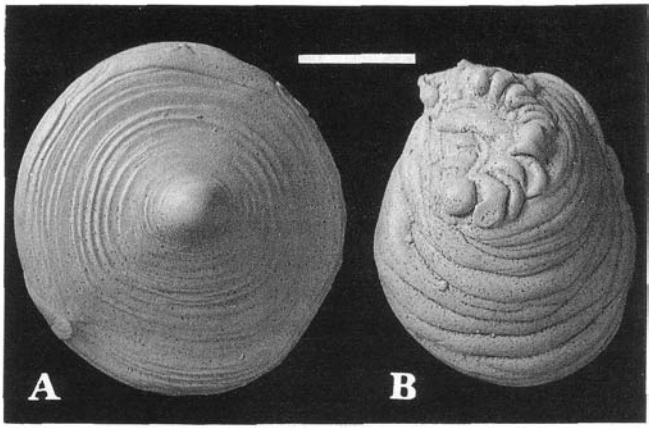

Fig. 3. ❑A. By pouring the molten wax freely from a fixed container, one may obtain patellifonn floats. ❑B. In the original candle experiment, an initial array of drops may create a broad base, on which accretionary growth builds a cup-shaped shell. This modification resembles *Gryphaea* specimens that remained attached beyond the larval state. Scale bar – I cm.

a particular problem, because they combine an echinoderm skeleton with a chordate bauplan (Jefferies 1986). Is it possible that similar symbiotic partners happened to induce the same kind of mineralization in two different clades?

Ecologic consequences. — The methaphor of the 'Garden of Ediacara' (McMenamin & Schulte McMenamin 1990) beautifully describes the ecologic situation of Vendian biota before the coming of skeletal animals. As seen in 'fossil snapshots' from Australia and Newfoundland (Seilacher 1992b), large but armorless and immobile Vendobionta inhabited sea bottoms in dense populations. Yet there is no sign that this easy prey became devoured by predators. On the other hand, trace fossils show that contemporaneous bilaterians were around, but lived below the sediment surface as small innocent deposit feeders. In shallow sandy habitats, there were also actinian-grade coelenterates with or without a stabilizing internal sand skeleton. But strangely not only true predators, but also filter feeders are so far unrepresented by Vendian fossils. In any case, the trophic chain must have been much simpler than in Phanerozoic times and the arms' race between predators and prey (Vermeij 1987, 1990) seems to have not yet begun.

Non-uniformitarian ecology, however, is not restricted to the interaction between larger Precambrian organisms, but concerns the primary producers as well. Below the reach of daily wave action, the upper millimeters of Precambrian clays, silts and sands appear to have been largely bound by microbes. Biostratinomic data (Seilacher & Pfluger, unpublished data) show that Vendobionta have been adhesively attached to this leathery substrate. Biomats also protected the sediment against event erosion or, in case it happened, led to the formation of sand and silt chips (Pfluger & Gresse unpublished data). Ubiquitous mat sealings must also have constrained the exchange between open water and the pore water underneath. The latter, presumably very low in oxygen, was the environment of the trace making infaunal worms that foraged horizontally – presumably on decaying lower tiers of the biomats.

The Cambrian revolution drastically changed this situation. Bioturbation by sediment-processing trilobites from above and by infaunal sediment feeders from below destroyed the matgrounds except in extreme environments. But in spite of intensified cropping, the constant vertical sediment mixing of biologically coated grains probably lifted primary bacterial bioproduction to a new, unprecedented level – as ploughing did in human agriculture.

Epilogue

Evolution at the organismic as well as the ecosystem levels is basically a synergetic phenomenon that can only partially be explained by the reductionist approach. This new perspective will inevitably revolutionize our view of earth history – not only in the field of paleobiology, but also in sedimentology and stratigraphy. Toni Hoffman, who had such a revolutionary mind, could participate only in the beginning of this intellectual turnover. Let us continue our work in his spirit!

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