Biological Versatility and Earth History

(evolution/fossils/morphology/higher taxa)

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ABSTRACT Examples from various plant and animal groups indicate that there has been a general increase in potential versatility of form, determined by the number and range of independently varying morphogenetic parameters, among taxa appearing at successively younger stages in the fossil record. Taxa or body plans with higher potential versatility have tended to replace less potentially versatile groups in the same or similar adaptive zone through time. Greater potential diversity allows for greater homeostasis, efficiency, and integration of structures and functions, and for an increase in size of the potential adaptive zone. In contrast, chemical versatility has generally decreased within groups from the pre-Cambrian to the Phanerozoic, partly as the result of apparent changes in the chemical environment and partly as the consequence of selection for efficiency and greater metabolic ease of handling of certain materials.

The purpose of the present report is to outline the evidence and implications for what may be a general trend in organic evolution, that of increasing potential versatility of form among related higher taxa or body plans of organization through geologic time.

The potential versatility of a given higher taxon or body plan is determined by the number and range of independent parameters controlling form. The nature of these parameters is often unknown at the biochemical or developmental level, but a satisfactory proximal understanding of their formal properties may be achieved by careful geometrical analysis.

In earlier work (1, 2), I have shown that the range of possibilities in gastropod shell form has increased through geologic time as the result of an increase in the number of controlling parameters. In uncoiled shells, which originated in the early Cambrian, two parameters are necessary to give a sufficient description of shell shape. These forms gave rise to planispirally coiled types in the Dresbachian stage of the Late Cambrian, in which the center of the generating curve traces a logarithmic spiral as it is swept through space and for which three parameters are required for a sufficient description. In the later Trempealeauian stage, planispirally coiled bellerophontacean gastropods gave rise to two stocks of conispirally coiled forms (3) whose shell may be described by six parameters. Both of these groups (Macluritacea and Pleurotomariacea) are characterized by shells in which the angle E between the plane of the aperture or generating curve and the axis of coiling is greater than 45°. In the latest Cambrian, shells of this type gave rise to forms in which the shell apex points more backwards than upwards (that is, E is less than 45°). The increase in the range of E brought with it a substantial increase in apertural shapes, sculptural types, and other elaborations of the outer lip that cannot be developed in shells with E greater than 45° (1, 2).

Together with the increasing potential versatility in gastropod shell form through geologic time, there is an increasing number of possible solutions to any given mechanical problem. High gravitational stability (the tendency for a shell to retain its orientation with the aperture down in the face of external forces) in uncoiled shells can be achieved only by an increase in the apical half-angle of the cone. The number of possible configurations exhibiting high gravitational stability rises to two in planispirally coiled forms, to three in conispiral types in which E is greater than 45°, and to four in those in which E is less than 45°. Each of the morphological solutions to the problem of attaining gravitational stability carries with it additional mechanical and geometrical properties, which make particular solutions more suitable to some habitats than to others. If the various parameters controlling shell form are allowed to vary during ontogeny, or if resorption and reprecipitation of shell material is possible, additional methods of achieving stability or other mechanical attributes become available.

Other examples of increasing potential versatility of form among related higher taxa, where one replaced or has evolved from the other, can be recognized from studies on a wide variety of organisms. Among tracheophytes, groups with regular dichotomous branching, which are first known from Upper Silurian rocks, gave rise to and were replaced by Late Paleozoic plants in which the process of overtopping produced a continuous main stem with shorter, generally helically arranged, lateral branches (4). The placement and relative size of lateral branches became highly variable among angiosperms, which arose in the early Cretaceous and have dominated the world's flora since the close of the Mesozoic. In actinopterygian fishes, the evolution of holosteans from palaeoniscoids in the later Permian was associated with increased flexibility of the upper jaw, resulting in a greater diversity of skull forms (5); a further reduction in upper-jaw rigidity among acanthopterygian teleosts in the Cretaceous led to an even greater versatility, including the first appearance of nonpredaceous types among bony fishes (5). Bakker (6) has shown that the ratio of proximal to distal limb-bone lengths among poikilothermic land vertebrates is always greater than 1, while in the homeothermic mammals and supposedly homeothermic dinosaurs it exhibits a far greater range in connection with the more varied modes of locomotion available to them. Dinosaurs and mammals, which arose in the Triassic, replaced poikilothermic tetrapods as the dominant large land animals in the later Mesozoic and Cenozoic (6). The evolution of posterior tubular inhalant and exhalant siphons among bivalve molluscs as a result of fusion of the mantle lobes led to a major adaptive radiation and increase

in form diversity after the Paleozoic (7). These and other cases generally involve an increase in the size of the potential adaptive zone for the more versatile group.

The examples of increased potential diversity of form through time that have been worked out in sufficient detail all refer to specific portions of organisms, such as shells, branches, skulls, and limb bones. While other structures and systems in these same organisms are geometrically often not well enough understood to permit analysis of their potential versatility of form, there is no compelling *a priori* reason to believe that evolutionary patterns in the versatility of these structures would be different from those for which such patterns have been elucidated. If increasing potential versatility through time is indeed a general trend in organic evolution, then it should be demonstrable with respect to many structures and systems in the same group of organisms.

The general evolutionary trend towards increased homeostasis or independence from external conditions (8, 9) and the tendency towards an increase in mechanical efficiency (5, 10, 11) and effectiveness of exploitation of continuously available resources (9, 12, 13) may both be understood in terms of increasing potential versatility. As the number of independent parameters controlling form increases, fewer adaptive compromises need to be made, and more functions can be optimized without detriment to other structures and functions (14, 15). The increased efficiency thus made possible may at the same time reduce dependence on the external environment, either by decreasing the lengths of periods during which resources are not taken up and assimilated or by allowing a greater amount of resource to be exploited during favorable times so that longer periods of inactivity can be tolerated. Taxa in which potential versatility has increased by the addition or extension of range of form-controlling parameters thus possess the potential for attaining greater efficiency and homeostasis, which are selectively advantageous in interactions with organisms possessing less potentially versatile body plans.

It is also likely that a greater potential versatility allows for more complex integration of structures and functions into a single unit or set of units. As Stebbins (16, 17) has pointed out, any genetic change leading to increased functional integration will be favored over one resulting in a breakdown of integration patterns, since the latter would generally reduce efficiency. Thus, by increasing the potential for complex integration and for optimizing more functions, an increase in the number and range of morphogenetic parameters can lead to greater independence from external fluctuations. It should be noted, however, that since integration implies a functional dependence of previously independent structures or parameters, more complex integration will decrease rather than increase potential versatility and lead to forms highly specialized to a particular mode of life (18, 19). In this connection it is interesting that the development of more versatile higher taxa with novel body plans very often occurs from a stock of small unspecialized organisms (20, 21) in which integration is apparently at a low level. As Thomson (14) has suggested in the case of the rhipidistian-tetrapod transition in the Devonian, new body plans may also arise by a process of correlative progression of structures and functions from one highly integrated system to another.

The trend towards an increase in potential versatility of form in successively younger stages of the fossil record stands in marked contrast to the pattern of chemical versatility. Hutchinson (22, 23) has noted that monerans, primitive protistans, and certain minute Metazoa (notably Turbellaria and interstitial Crustacea) exhibit a high degree of evolutionary euryhalinity, that is, the tendency for members of a given family, genus, or even species to live in both fresh or salt water. With an increase in body size, representatives of these groups often became restricted to either fresh or salt water (22, 23). The possibility cannot be ruled out that much of the early evolution of life took place in waters of variable or reduced salinity compared with those of Phanerozoic seas, and that the observed evolutionary euryhalinity in these primitive organisms is therefore a reflection of ancient environments (23) that may be rare or even absent in the Recent and to which the principle of uniformitarianism may be inapplicable. Shapiro (24) and Brock (25) have shown that the evolutionarily euryhaline blue-green algae are much less versatile with respect to pH and CO_2 than are the eukaryotic green algae. Among certain groups of higher animals, there is a tendency for euryhalinity at the familial, generic, or specific level to occur within the more recently evolved, more versatile taxa (mesogastropod and pulmonate molluscs, demosponges, and vertebrates), while such older and morphologically less versatile groups as the archaeogastropod molluscs, calcarean and hexactinellid sponges, and echinoderms were and are restricted to marine waters (22, 23).

Organisms in the latest pre-Cambrian and early Phanerozoic used a wide variety of substances in the construction of their skeletons, including silica, strontium sulfate, calcium carbonate, calcium phosphate, and probably chitin. Groups originating later in the Phanerozoic have used only the three last-named materials and (in vascular plants) cellulose and lignin for construction of supportive tissues. The lower diversity of skeletal substances among the more recent higher taxa may again be related to differences between pre-Cambrian and later Phanerozoic chemical environments or to the abundance and metabolic ease of handling of the various materials. Similarly, the considerable diversity of sources for chemical energy among monerans has not been retained among multicellular organisms in the Phanerozoic (26, 27).

In summary, an increase in versatility of form in the more recently evolved taxa as compared to the more ancient ones permits the development of greater homeostasis, efficiency, and functional integration, and generally leads to an increase in size of the potential adaptive zone. Morphologically more versatile taxa or body plans have tended to replace the less potentially versatile taxa through time in the same or similar adaptive zone. In contrast, chemical diversity has generally decreased within higher taxa from the pre-Cambrian to the Phanerozoic, partly as the result of apparent changes in the chemical environment and partly as the consequence of selection for efficiency and ease of metabolic handling.

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