A DESIGN SPACE FOR ANIMAL SKELETONS: IMPLICATIONS FOR PATTERNS OF MACROEVOLUTION

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Organic design arises, on every scale, by the spontaneous self-organization of successively more complex structures from simpler subsidiary components. The resulting structures converge repeatedly on architectural designs that can be constructed by growing organisms, and that are viable but not necessarily optimal in relation to any one function. Empirical observations and theoretical models of developmental processes suggest that these recurrent elements of design are fixed point attractors which organic dissipative structures must necessarily approach. We characterize these structures as topological attractors, thereby emphasizing that they are determined by the properties of matter and the geometry of space-time.

We have derived a set of potential designs for the elements of animal skeletons, in terms of geometric rules, growth processes, and the properties of materials. Skeletons or components of the skeletons of actual living and extinct organisms are matched with the possibilities defined within this theoretical morphospace. The extent to which the skeletal components of individual organisms are differentiated, exploiting various parts of the skeleton space, provides a crude metric of structural complexity. The skeleton space serves as a common context, in which we can compare the extent and pattern of exploitation of this range of potential organic designs, from one taxon to another.

Our analyses show that the most evolutionarily advanced animals in a given class or phylum generally do not have the most complex skeletons; that molluscs and vertebrates are more morphologically diverse than arthropods; and that the physical constraints of life on land and in the air substantially limit the variety of skeletal structures suitable to be employed by animals living in these environments. Moreover, when the skeletons of all known animals, living and extinct, are considered together, we find that the total range of possible skeletal designs has been very fully exploited.

These results strongly support the hypothesis that the essential elements of organic design are inherent in and predictable from the material properties of the universe. Environmental and demographic circumstances, invariably involving a large element of chance, together with the constraints of phylogenetic history largely determine the course of evolution in individual lineages. In contrast, structural principles such as those delineated here determine the recurrent themes of organic design, over large numbers of taxa and long periods of time. Thus, it is no accident that two major groups of animals that have most successfully exploited jointed lever skeletons, vertebrates and arthropods, have achieved the most diversified adaptive radiations, in the sea, on land and in the air.

Among the structural paradigms defined within the skeleton space, stronger and weaker topological attractors may be identified empirically by the frequencies with which particular design elements have evolved independently, in unrelated taxa. Plausible functional or constructional rationales can readily be devised, ex post facto, to explain the repeated convergence of organic structures on some obvious strong topological attractors, such as branching networks, spiral cones, and bivalved shells. Unfortunately, it seems unlikely that an analytical method can be devised to predict these strong attractors a priori, as the variables involved cannot all be quantified in the same way.