

ON THE GROWTH OF ORGANISMAL COMPLEXITY

Summary

The genetic reduction or “genocentrism” of the Synthetic Theory of Evolution was uncondusive to its integration with evolutionary morphology and did not leave any room for even addressing the complexity of organisms. For the same reason the concept of function was effectively ignored in the conceptual scheme of this theory that pooled all phenotypic and genetic determinants of reproductive success under the heading of fitness. In fact the concept of function is critical to understanding the complexity of any goal-directed system and the growth of organismal complexity comes down to an increase in the number of functions even it may be easier to measure by morphological diversity. It is a great realization of the 20th century that body parts at all levels are commonly coopted to new functions and thus genuine multifunctionality (i.e., performing multiple, discrete and unrelated functions) is constantly generated by an evolving organization. What seems to be less well understood is that new functions arise from ubiquitous nonfunctional interactions of body parts with their environment that may be external (Umwelt, niche) or internal (milieu intérieur) to the organism. While these interactions arise as inevitable causal by-products of a structure's functioning or static properties, their impact is accidental to any organismal needs (that is, ultimately, any current functions) and only sometimes happens to be useful in which case an interaction becomes a function. The is exactly the way mutations are used by natural selection, hence the dynamics of nonfunctional interactions that are generated by body parts is considered here to be a major factor of evolution and referred to as parafunctional variation. The growth of complexity as observed in the evolution of organisms would not be possible without multiplication of parts. This is because cooptions to new functions lead to adaptive (and sometimes also direct, functional) conflicts with old ones and because

all functions tend to be crude and generalized (euryfunctional) at the beginning and need refinements through a subdivision of tasks. The escape from adaptive conflict between unrelated functions (as acquired via the mechanism of cooption) is resolved through Dohrn's exchange of functions between duplicated structures (serial homologues or paralogues) where one of them takes over a minor function of the ancestral structure and becomes adapted to it as to the main function. Most cases described as neofunctionalization of duplicated genes are in fact cases of the exchange of functions. Refinements of generalized functions are achieved by the way of Severtsov's subdivision of function into partial tasks or subfunctions, which generates the complexity of organismic apparatuses (e.g., osteomuscular devices) and molecular quaternary structures such as heteromers that arise by duplication and coaptation of molecules (as in the heterotetramers of hemoglobin). Some cases described under the heading of subfunctionalization fall into this category while others represent cases of simple divergence of paralogues under independent expression control. The latter is facilitated by the mobility of genomic sequences and the relative freedom of association between regulatory and structural genes. Other than that, the complexity of both organs and molecules seems to evolve under similar rules that have yet to be better understood and integrated. The combined action of natural selection, genetic variation, and parafunctional variation is deemed sufficient to explain the evolutionary growth of complexity. While natural selection seizes upon any beneficial effects including those afforded by the thermodynamic propensities of organic configurations, there is no good reason or evidence to believe in the spontaneous generation of higher levels of organization such as multicellularity.