A

Anagenesis

Robert Lickliter
Department of Psychology, Florida International University, Miami, FL, USA

In the general sense, evolution can be characterized by three distinct phenomena: (1) adaptation, the remarkable fit between an organism and its environment, (2) diversity, the great variety of extinct and extant organisms, and (3) complexity, the intricacy of the organization of internal and external structure and function (Muller and Olsson 2003). *Anagenesis* refers to the idea that there are directional trends in this complexity. In particular, a hierarchy of increasing levels of organization from the simple to the complex characterizes the diversification of species. As Dobzhansky et al. (1977, p. 236) put it in their classic text *Evolution*, anagenesis creates "organisms with novel characters and abilities beyond those of their ancestors." In evolutionary biology, anagenesis refers to the progressive evolution of a species resulting in linear descent (phyletic divergence); in contrast, cladogenesis refers to speciation by evolutionary splitting of a lineage (branching) to additional species.

The concept of anagenesis has also been used in comparative anatomy, comparative physiology, comparative endocrinology, as well as comparative psychology (Rensch 1959). Rensch identified several defining features of anagenesis, including: (1) increased complexity (differentiation), (2) centralization of structures and functions, (3) special complexity and centralization of the nervous system, (4) increased plasticity of structures and functions, and (5) increased independence from the environment and increasing command of environmental factors (progression of autonomy). Of course, independence from the environment is a relative concept, as no organism is ever free from its environment. When applied to the comparative study of behavior, anagenesis has typically referred to the progressive evolution of adaptive behavior, learning ability, or cognitive capacity that is often accompanied by the emergence of new psychological capacities (Gottlieb 1984).

The steps or units of anagenesis are typically referred to as "grades" or, in some cases, "levels" (Aronson 1984). A grade or level can be seen as an ascending series of improvements or increases in complexity of any structural or functional unit of analysis within animal groups that may or may not be closely related from a phylogenetic standpoint (Gottlieb 1984). Grades or levels thus address the ranking of behavioral organization (i.e., ability to exhibit various forms of learning, levels of exploratory behavior) relatively independent of strict evolutionary lineages (phylogenetic relationships). As a result, anagenetic analysis has been used most successfully to characterize grades or levels of behavioral complexity at the supraspecific level, that is, across genera, families,

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orders, or classes, rather than at the level of species. Examples include patterns of organization of the nervous system, increases in developmental plasticity, and improvements in behavioral versatility or adaptability to environmental change (Yarczower 1998). For example, within the order Chiroptera (bats), researchers have demonstrated that the relatively large brain observed in some bat species is associated with adaptations used to feed on energy-rich foods that are often unpredictable in their spatial distribution (Eisenberg and Wilson 1978). Such descriptions of the specific fit between phenotypes and environments across genera provide a foundation for further studies of both adaptation and diversity.

Schneirla (1949) was among the first comparative psychologists to promote the importance of levels of psychological capacities to frame the comparative study of animal behavior. His anagenetic concept of levels (see Greenberg, this volume) emphasized the value of recognizing and assessing the range of differences in complexity, degree of development, and organization of behavior functions across different types of animal species. This type of approach has been termed "pheneticism" within evolutionary biology (Harvey and Pagel 1991), where grade or level is determined by similarity in phenotypic characters or traits rather than by phylogenetic relationships (common ancestry). For example, Tobach and Schneirla (1968) proposed a hierarchy of behavioral levels based on social and psychological organization: taxis, biotaxis, biosocial, psychotaxis, and psychosocial (see Greenberg, *Behavioral Levels*, this volume). Using this hierarchy, Greenberg (1995) noted that in the general sense, animals demonstrate less behavioral plasticity or versatility function at lower behavioral levels (i.e., taxis, biotaxis), whereas they demonstrate more behavioral plasticity or versatility function at higher behavioral levels at which psychological processes influence the course of behavioral development (i.e., psychotaxis, psychosocial). Importantly, increased behavioral plasticity is highly correlated with increasing nervous system size, complexity, and organization (Jerison 1973; Jerison and Barlow 1985). Gottlieb (1984) extended this approach to anagenesis by emphasizing that developmental plasticity and behavioral versatility are useful hallmarks of progressive behavioral evolution. He argued that application of this perspective allows a measure of anagenesis to be obtained by comparing different animals' behavioral adaptability in response to experimentally altered ecological conditions or challenges. However, this ecologically based approach to testing anagenesis has received little research attention to date.

The concept of anagenesis and its use of grades or levels to compare behavioral evolution across animal species independent of strict evolutionary lineages have not been without criticism within comparative psychology (i.e., Capitanio and Leger 1979; Hodos and Campbell 1969, 1990). It is certainly the case that objective criteria for how to best distinguish successive grades or levels of developmental plasticity and behavioral versatility remain poorly defined. Hodos and Campbell (1969, 1990) see comparing evolutionary trends across groups of animals that are not closely related by way of common ancestry as overly subjective and even unscientific. They argue that most comparative psychologists do not base their work on strict evolutionary lineages (i.e., phylogenetic trees), which they view as the appropriate subject matter of a genuine comparative psychology. While such criticisms have been challenged (e.g., Gottlieb 1984; Greenberg 1995), it is clear that an objective description of the criteria used to identify differences in behavioral plasticity or versatility between higher and lower grades of animal species is crucial to the merit and usefulness of anagenetic analysis. Given that the comparative method has been the most general and effective technique for asking questions about the patterns of evolutionary change from Darwin to the present, comparisons of animal behavior and cognition using *both* evolutionary trends and evolutionary lineages will likely provide a deeper understanding of the phenomena of adaptation, diversity, and complexity.

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