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[REVIEW]

Ecological Aspects of the Evolutionary Processes

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ABSTRACT—Darwin in his *On the Origin of species* made it clear that evolutionary change depends on the combined action of two different causes, the first being the origin of genetically based phenotypic variation in the individual organisms comprising the population and the second being the action of selective agents of the external environment placing demands on the individual organisms. For over a century following Darwin, most evolutionists focused on the origin of inherited variation and its transmission; many workers continue to regard genetics to be the core of evolutionary theory. Far less attention has been given to the exact nature of the selective agents with most evolutionists still treating this cause imprecisely to the detriment of our understanding of both nomological and historical evolutionary theory.

Darwin was vague in the meaning of his new concept of “Natural Selection,” using it interchangeably as one of the causes for evolutionary change and as the final outcome (= evolutionary change). In 1930, natural selection was defined clearly as “non-random, differential reproduction of genes” by R. Fisher and J.B.S. Haldane which is a statement of the outcome of evolutionary process and which omits mention of the causes bringing about this change. Evolutionists quickly accepted this outcome definition of natural selection, and have used interchangeably selection both as a cause and as the result of evolutionary change, causing great confusion. Herein, the details will be discussed of how the external environment (*i.e.*, the environment-phenotype interaction) serves as selective agents and exerts demands on the phenotypic organisms. Included are the concepts of fitness and of the components of fitness (= adaptations) which are respectively (a) survival, (b) direct reproductive and (c) indirect reproductive features. Finally, it will be argued that historical-narrative analyses of organisms, including classification and phylogenetic history, are possible only with a full understanding of nomological evolutionary theory and with functional/adaptive studies of the employed taxonomic features in addition to the standard comparative investigations.

Key words: evolution, fitness, adaptation, classification

INTRODUCTION

When Darwin published his theory of evolution by natural selection in his *On the Origin of Species*, he actually proposed a bundle of five independent theories (Mayr 1985). For the first half century following Darwin, emphasis was placed largely on his theory of common descent, the second of the five theories discussed by Mayr (1985:758–761) and the only one of these five theories that falls under the heading of historical-narrative explanations. Almost no interest existed among biologists in the mechanisms of selective agents and other interactions between living organisms and their external environment. Evolutionists all

but ignored the other four theories presented by Darwin in 1859, especially the causes of phyletic evolutionary change, which are clearly nomological-deductive explanations (Bock 2000); nomological referring to ‘law-like statements.’ Darwin emphasized that the two causes for phyletic evolutionary change are, using modern terminology, (a) the appearance of hereditary phenotypic individual variation in the population and (b) the demands of selective agents on these varying individuals. Although these two mechanisms have been stressed over and over again by evolutionists, the greatest emphasis ever since 1859 has always been on the genetic aspects of evolutionary change - how new genetic variation originated, how it was transmitted from one generation to the next, and how the pattern of genetic variation in the population changed over the course of time. This focus on the genetic aspects of evolutionary change started immediately

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in 1859 because almost nothing was known about the origin and transmission of genetically-based phenotypic variation and because most biologists, then as well as now, worked in the laboratory and had little to no interest in organisms living in their normal environment. This distorted, gene-centered approach to evolutionary thinking became even greater with the development of Mendelian genetics after 1900. Even today, many biologists and philosophers of science consider genetics to be the core of evolutionary analyses (Dawkins 1976, 1982; Sterelny and Griffiths, 1999), and/or define evolution naively as 'Evolution is nothing but changes in gene frequencies.' (Hull, 2001:13).

Interest in the multiple set of interactions between living organisms and their external environment lagged well behind and their comprehension is still inadequate. I have discussed the spectrum of organism-environment interactions (see Fig. 1) and their roles in evolutionary mechanisms (Bock, 2002a), pointing out that three distinct interactions can be recognized, namely: (a) The environment-genotype acting as mutating agents on the genotype, and leading to modifications (mutations) of the inheritable material; (b) The environment-ontogeny acting as paragenetic agents both during and after ontogeny, and bringing about modifications in the realized phenotype of the individual organism on which selective agents act. This interaction has scarcely been considered by evolutionists although it has a most sig-

nificant role in the environment-phenotype interaction and in evolutionary changes of all attributes of all organisms; and. (c) The environment-phenotype acting as selective agents on the phenotype, and resulting in modifications in the characteristics of the population or the species over evolutionary time. The last is the basic interaction between the external environment and organisms considered by evolutionists, but this consideration is largely 'lip-service' without inquiry into the details of individual attributes. Indeed, the overwhelming response to any discussion of particular adaptations and associated selective agents remains one of great skepticism and excessive demand for support of the particular selective agent and its interaction with the phenotypic feature.

Herein I will focus on: (a) Those interactions between the phenotypic organism and the external environment with emphasis on selective agents arising from the external environment and placing demands on features of the organism, which are part of nomological evolutionary explanations; and (b) Their significance for clarifying evolutionary histories and classifications which are historical evolutionary explanations (Bock, 1981, 1991a, 2000, 2003). I should stress that all historical-narrative explanations in science are completely dependent on well-tested, underlying nomological-deductive explanations. The goal of the historical-narrative explanations is to present credible hypotheses that are strongly supported by empirical observations.

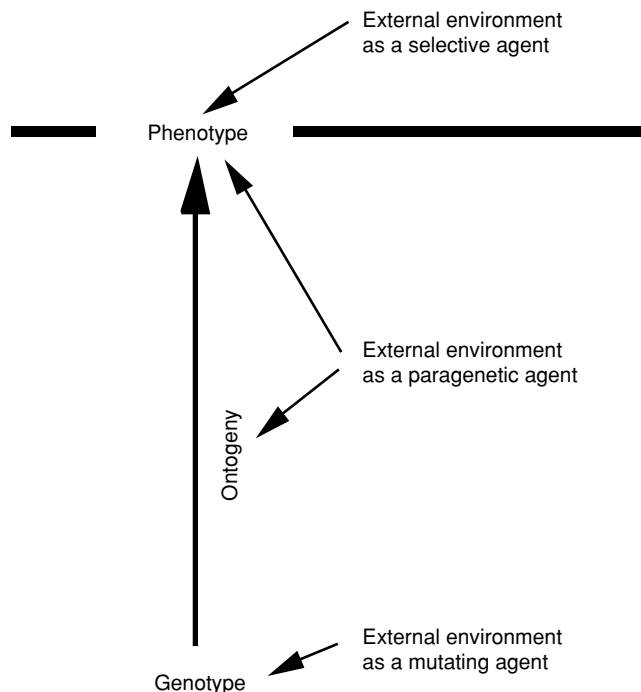


Fig. 1. Schematic diagram showing the relationships between the genotype and the phenotypic of an organism and its external environment acting as a mutating agent on the genotype, as a paragenetic agent both during and after ontogeny, and as a selective agent on the phenotype. The heavy horizontal line to each side of the phenotype indicates the possible range of phenotypic expression resulting from the action of the external environment as a paragenetic agent. (Figure taken from Bock, 2002a).

SELECTIVE AGENTS AND COMPONENTS OF FITNESS

Unfortunately Darwin used natural selection (= selection) in at least two different ways in his *On the origin of Species*. Basically he considered this concept as the environmental cause placing demands on the varying members of a population, choosing between them and hence bringing about evolutionary change. But his clearest definition of natural selection (Darwin, 1859:61: 'I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection.') is an outcome definition, not that of a cause. [I will not quibble with anyone who disagrees with my interpretation of this sentence and of the paragraph from which it was taken because of the frequent lack of clarity in Darwin's writing style. Darwin wrote the *Origin* rapidly between August 1858 and May 1859, and any editing was almost completely limited to Emma Darwin and some women friends (Browne, 2002:76).] When population geneticists first formulated a mathematical-genetic theory of evolutionary change (Bock, 1993:11–14), they quite reasonably chose this wording, and hence defined natural selection as *non-random differential reproduction of genes*. No cause for this differential reproduction is given in this definition of selection; there can be several possible causes in addition to selective agents which can result in natural selection. The definition of non-random differential reproduction of genes has been broadly accepted, but has also left biologists without a term for 'selection' as a cause. Consequently, the term

natural selection (or simply selection) is used by most evolutionists simultaneously for one of the causes of evolutionary change and for the outcome - the resulting evolutionary change - leading to major confusion in evolutionary theory. Hence, I suggested the term selective agent for the cause that Darwin implied in most places in his 1859 book when he used 'natural selection' or 'selection.' Selective agents

arise from the external environment of the organism and place demands on the organism. These agents do not arise unilaterally from the environment, but depend on how the organism interacts with particular environmental factors (Bock and von Wahlert 1965; Bock 1980). Diverse organisms can interact differently to the same environmental factor and hence be subjected to the demands of quite distinct

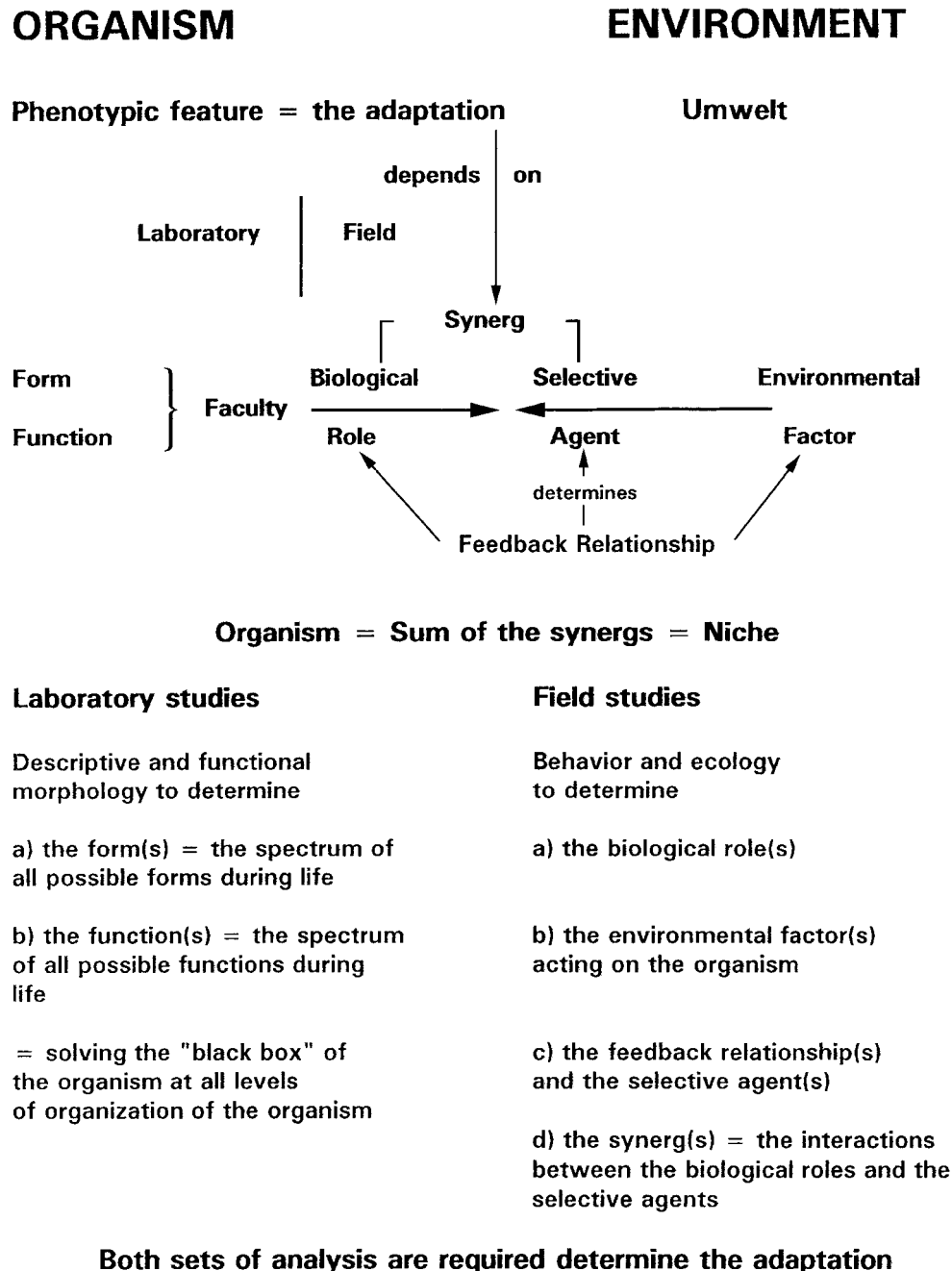


Fig. 2. Simplified diagram to illustrate the components of an adaptation and the range of laboratory and field studies required for the nomological determination of an adaptation. The adaptation is a phenotypic feature of an organism and depends on the properties of the synerg, *i.e.*, the adaptation is judged relative to a selective agent arising from the external environment. The selective agent, placing a demand on the phenotypic organism, but the exact nature of the selective agent is determined by a feedback relationship between the organism and the environmental factor via the biological role. After the adaptation has been established, further study is needed to assess its degree of goodness. (Figure modified from Bock, 1980).

selective agents. Adaptations and adaptive evolutionary change are judged with respect to selective agents, arising from the external environment (Fig. 2).

One of the central reasons behind Darwin's thinking about organic evolution was to provide a scientific explanation for the concept of adapted attributes of organisms and how these adaptations came into being. Biologists had a clear understanding of adaptations well before 1859 as features which are well adjusted to the demands placed on the organism by the external environment, but did not have a scientific explanation of how these adaptations came into being. The concept of adaptation should be restricted to phenotypic features of organisms; adapted features permit the organism to interact positively to the demands placed on it by selective agents. Adaptive evolutionary changes are those taking place under the actions of selective agents. The concept of adaptation, covering all phenotypic attributes positively interacting with selective agents, is thus exceedingly broad; indeed the definition of adaptation is often redundant, or at least circular, with the concept of fitness of individual organisms. Some workers (Ehrlich and Holmes, 1963) argued that both the concepts of fitness and of adaptation are not necessary and suggested that one be dropped; this point is logical, but not satisfactory. Although the concepts of adaptation and fitness are closely interconnected in evolutionary theory, they differ from one another and should be carefully defined as independent parts of nomological evolutionary theory.

I proposed a solution (Bock, 1993:19–22) to this conundrum by showing that the fitness of an individual is related to its suitability (= fitness as used by Darwin; a 'suited individual' is the same as Darwin's 'fit individual') which is determined by components of fitness; these are the diverse phenotypic features of the organism. In this earlier paper (p. 19), I used the terms 'competency' for 'suitability' and 'elements of competency' for 'components of fitness,' but feel that the latter terms are better. Fitness and suitability are statistical concepts obtained by observations over a number of individuals of different kinds of organisms. Hence individual organisms in a population possessing the best adaptations will statistically be those having the best suitability and the best fitness. Note that those individuals possessing statistically the best fitness must have *both* better survival and better reproductive features; having only better survival features is insufficient if the individual has poor reproductive features. These components of fitness (= adaptations) are (a) survival features, (b) direct reproductive features, and (c) indirect reproductive features. Adaptations are evaluated relative to selective agents, not to environmental factors as the same environmental factor can result in different selective agents acting on the organism and hence producing different adaptations. Although the term 'adaptation' has been used generally for 'survival features' (Bock and von Wahlert, 1965; Bock, 1980) this term is best used in the more general sense for components of fitness. Adaptations can be defined as: *any phenotypic features of the individual organ-*

ism which statistically increase the fitness of that individual relative to other individuals in the population. And as noted above, to have a positive fitness an individual must have both survival and reproductive features.

Herein I wish to summarize the analyses of survival features (previously called adaptations in my earlier papers; Bock and von Wahlert, 1965; Bock, 1977, 1979) and of reproductive features, and to show how these apply to historical evolutionary explanations such as classification and phylogeny. A significant problem is to determine whether a particular attribute in an organism is a survival or a reproductive feature, either direct or indirect. Many attributes which have been considered as survival features are actually reproductive features. And in a number of cases, the same feature can be a survival feature in one group and a reproductive feature in another. Some features may serve both as survival and reproductive features in the same organism. Sorting out these possibilities is a difficult task, and one that has scarcely been considered by evolutionists.

For ideas about preadaptation and paradaptation, see Bock (1959, 1967, 1979).

COMPONENTS OF FITNESS

Suitability (= competency) was coined as a replacement for Darwin's original term of fitness, now used in modern evolutionary theory as a measure of the contribution by an individual to the gene pool of the next generation. Suited individual organisms have the same meaning as fit individuals as used by Darwin (1859). Suitability is a characteristic of individual organisms and depends on the individual phenotypic attributes (= adaptations) of the individual; they include survival features, direct reproductive features and indirect reproductive features. I will consider discuss adaptations mainly as survival features in terms of morphology, but the following comments hold equally for reproductive features and for all phenotypic attributes of the organism. As such, morphological attributes are not adaptations to other attributes of the organism or to functional properties of the attribute. Wings are not adaptations for flight. Adaptations are only judged with respect to selective agents arising from the external environment and acting on the individual organism.

The core thesis of nomological evolutionary theory, as clearly stated by Darwin (1859:61), is that those individuals in a population possessing the best combinations of components of fitness (= both survival and reproductive features) would have statistically the greatest fitness, and hence would statistically pass these attributes to the next generation if they are at least, in part, heritable. Fitness can be measured relatively easily, but establishing the existence of particular adaptations and their degree of goodness is far most difficult, and has rarely been attempted by biologists.

Survival features are associated with the continued survival of the individual organism as an individual and serve to permit survival of the organism until it can reproduce. A sur-

vival feature can be defined as: *A phenotypic attribute of an organism that has a role in the life history of that organism (i.e., must preform some definite task such as obtaining food or escaping from a predator) and must preform this role with a certain degree of efficiency.* Hence a survival feature is always part of the phenotypic organism and it is a form-function complex (= a faculty) of a feature having a biological role and interacting with a selective agent of an environmental factor of the Umwelt of that organism (Bock and von Wahlert, 1965).

Survival features are not the only component of fitness. In addition, there are direct reproductive features (for the production of direct offspring) and indirect reproduction features (for the production of collateral offspring; sometimes called kin selection, see Brown, 1987); these reproductive features include but are not synonymous with those associated with the concept of sexual selection first proposed by Darwin. Both types of reproductive features are associated with the production of offspring, and are frequently in direct conflict with survival features. A direct reproductive feature can be defined as: *A feature of an organism having properties of form and function which permit the organism to produce direct offspring (= descendent kin) successfully under the action of the selective agents of the external environment of that organism.* An indirect reproductive feature is defined in the same way but with the substitution of '*indirect offspring (= collateral or non-descendent kin).*' A large number of attributes of organisms are reproductive features, not survival features. These embrace the entire reproductive system (including the time of breeding, endocrine control, etc.) courtship display, parental care, as well as many features that may appear at first glance to be survival features, but actually serve to produce offspring.

It is necessary to go beyond general statements about adaptations to establish a sound theoretical framework for the concept of adaptation as well as the details of individual examples. Determination of particular survival features requires careful morphological description, based on a knowledge of what is essential for functional investigations, and functional analysis preferably based on direct observations. Descriptions must include understanding of the exact relationships between properties of morphological form and function. For example, it is necessary to determine the relationships between morphological properties, such as fiber length, total fiber cross-sectional area and fiber arrangement, in muscles and functional properties, such as maximum force, speed, distance of shortening, and relative force development with length changes during contraction (Bock, 1974, 1991b). Observations are needed of the organism living in its natural environment (with an understanding that the environment could have been changed significantly in historical times) so that decisions can be reached about the selective agents and their demands acting on the organism (see Fig. 2).

From these observations and inferences, conclusions can be made whether the phenotypic feature is a survival

feature. These conclusions about the existence and goodness of survival features are clearly nomological-deductive explanations, without any consideration of the 'historical' origin of the phenotypic attribute as a survival feature. The notion of exaptation (Gould and Vrba, 1982) is simply nonsense because it is immaterial how particular adaptations, be they survival or reproductive features, come into being. Advocacy and use of the concept of exaptation results from the failure to distinguish between nomological and historical evolutionary theory. A feature is an adaptation with respect to a particular selective agent regardless of how it came into being just as much as water is water regardless of whether it came into being by the combustion of hydrogen in the presence of oxygen or the decomposition of hydrogen peroxide into water and oxygen. In a similar fashion, many workers, especially philosophers of science, have confused function with adaptation and have claimed that functions of particular phenotypic attributes can be ascertained only by a consideration of their evolutionary past. [See Bock and von Wahlert (1965) for definitions of function and biological role as well as their distinction from adaptation.]

The analysis of particular survival and reproductive features is usually a most difficult task, and the search for the adaptiveness of a phenotypic attribute must not be abandoned if a solution cannot be reached quickly. Identifying individual adaptations can be done only with actual observations of the organism living in its normal environment which is not always easy to do, and which is not feasible for many Recent organisms and for all fossils. It is not valid to ascertain adaptations by a morphological comparison of similar features in different species because morphologically dissimilar features to be adaptations to the same selective agent in different organisms (= paradaptations) and morphologically similar features to be adaptations to different selective agents (Bock, 1967). Thus evolutionists, ever since Darwin, were in error by assuming that the same selective agent acting on different organisms will always result in the same adaptation. A feature can be an adaptation to several different selective agents so that the common argument that a particular feature must be an adaptation only to one selective agent is simply not valid. Avian feathers are adaptations to selective agents associated with heat loss and excessive heat gain, with flight (both as airfoils and a streamlined body shape), with protection against water, etc. The discussion that a divaricating habit in about 10% of New Zealand trees is an adaptation to selective agents associated *either* with protection against grazing by the now extinct moas (Aves: Dinornithidae) *or* against extremes of climate (Greenwood and Atkinson, 1977; Anderson, 1989) is not valid. This growth form could be an adaptation to both selective agents. Whether this growth habit originated in response to one or the other of these selective agents is a completely different question, and one that is usually confused with the several possible adaptive significances of the phenotypic attribute.

After an attribute has been demonstrated to be an

adaptation to a particular selective agent, it is necessary to estimate its degree of goodness in different individuals of the population. This can be done for survival features by ascertaining the amount of metabolic energy required to maintain the synergical connection between the biological role of the feature and the selective agent with a smaller amount of energy indicating a better degree of adaptiveness (Bock and von Wahlert, 1965) or several additional ways (Bock, 1980). It is even more difficult to judge the degree of goodness of reproductive features independently of the statistical value of fitness of the individual; even suggestions of how to make such measurements are formidable. To my knowledge, measures of the goodness of adaptations have rarely, if ever, been attempted by biologists; hence it is not possible to correlate statistically a better degree of adaptation of phenotypic features with a greater fitness of the individual organism.

EXAMPLES OF ADAPTATION

In the following examples, observations of the functions and biological roles of features in organisms living in their natural environment form important parts of the analysis of these adaptations. The same phenotypic attribute can be a survival feature to quite different selective agents and/or serve as survival or reproductive features in diverse organisms or even in the same organism.

(a) The damselfly penis

This feature should be mentioned because it first provided me with the realization that a distinction exists between survival and reproductive features. Waage (1979) described the penis of the damselfly, *Calopteryx maculata* (Odonata) as having a spoon-like shape. He showed that this particular penial morphology functioned to permit the male to scoop out of the female sperm storage organs the sperm deposited there from previous matings and discard it before depositing his own sperm there. The penis also serves as the sperm transfer organ. The last male to copulate with a particular female damselfly will fertilize most of all of the eggs of that female. This particular spoon-like morphology of the penis cannot in any way serve as a survival feature — it is purely a direct reproductive feature. A similar adaptation existing in a number of mammals is the property of the semen to harden in the vagina of the female after copulation, forming a vaginal plug and hence preventing other males from depositing their sperm.

(b) The avian intramandibular hinge

Many birds possess a vertical hinge somewhere in the middle (anterior-posterior) of both mandibular rami which allows the bird to bend both rami outward, thereby increasing the distance between them and hence the size of the object that can pass into or out of the esophagus (Bühler, 1981). In most groups (i.e., herons, Ardeidae; pelicans, Pelecanidae; nightjars, Caprimulgidae), the intramandibular hinge is clearly a survival feature, permitting the bird to swallow larger food items, although in Barn Owls (*Tyto*) it serves

to allow the bird to regurgitate a larger pellet of bones and hair from its stomach. Yet this hinge is a reproductive feature in pigeons (Columbidae) which feed their young 'crop-milk' and must have a sufficiently wide gap between the two mandibular rami so that the young bird can thrust its head into the mouth of the adult to reach the crop. In some birds, such as herons, the intramandibular hinge may also serve as a reproductive feature, allowing the young bird to insert its head into the esophagus of the adult to obtain food. Possibly in some of the fruit-eating pigeons, this feature is also a survival feature for feeding on larger fruits. Note that the avian intramandibular hinge is a reproductive feature in some birds and a survival feature to different selective agents in others.

(c) Nutcracker sublingual pouch

The nutcrackers (*Nucifraga*: Corvidae) possess a large pouch in the floor of the mouth, opening in front of the tongue (Bock, Balda and Vander Wall 1973). During the fall harvest of pine seeds, the pouch is used to increase greatly the number of seeds an individual can carry on each trip up to the communal caching area higher in the mountains (*Nucifraga columbiana*). The stored seeds are used during the next breeding season to feed the incubating adult and especially the young birds, thereby allowing this species to breed early in the spring before the deep snows are fully melted. Hence, the sublingual pouch is a direct reproductive feature, not a survival feature. Whether the sublingual pouch also serves as a reproductive feature in the Eurasian nutcracker (*Nucifraga caryocatactes*) is not known. This pouch is a specialization of a diverse series of features in different species of the Corvidae for carrying food to be stored which are usually survival features in these other corvine species.

(d) Oral mucus glands

Enlarged mucus-secreting glands are found in a number of diverse groups of birds with the mucus varying from a watery fluid to a thick, sticky material. In woodpeckers (Picidae) the mucus serves to assist capturing food with the sticky tongue. In the gray jays (*Perisoreus*: Corvidae), it serves to glue together small bits of food into a bolus which is then stuck to a tree branch to provide a food supply during bad winter weather (Bock, 1961; Dow, 1965), again a survival feature. However, the mucus-secreting glands in diverse species of swifts (Apodidae) is used to glue twigs and other plant material together to construct their nest which is glued to a vertical surface. In the most specialized swiftlets (*Collocalia*: Apodidae) the nest is constructed entirely of spun mucus threads which harden to form a cup-shaped nest, the basis of 'bird's nest soup.' In the swifts, the enlarged mucus-secreting oral glands are clearly a direct reproductive feature. Again oral mucus glands are a direct reproductive feature in swifts and a survival feature to different selective agents in other birds.

(e) Secondary articulations of the avian jaw

As in most species of vertebrates, birds possess a kinetic skull in which the original upper jaw and bones attached to it move with respect to the original chondrocranium.

nium and bones attached to it (Bock, 2002b). A series of jaw muscles and ligaments control the complex pattern of movements of the upper jaw in addition to the lower jaw. Difficulties exist if the feeding method of the particular species involves holding the lower jaw fixed in place while raising and lowering the upper jaw. In a large number of avian families (but not necessarily in all species within particular families), the mandible articulates directly with the brain case, either between the posterior end of the mandibular ramus and the base of the skull (Bock, 1960) or in the Australian honey-eaters (Passeriformes: Meliphagidae) between the dorsal edge of the mandibular ramus at its midpoint and the ectethmoid plate in front of the eye (Bock and Morioka, 1971). In all birds possessing a secondary articulation of the mandible, the function of this articulation is the same, serving as a brace to hold the lower jaw in position while allowing opening and closing of the upper jaw with a minimum of muscular effort. This is especially nicely shown in the skimmers (*Rynchops*; Laridae: Rynchopinae) which catch fish by flying just above the water surface and skimming with their knife-like lower jaw that must be held in place against the force of the water (Zusi, 1962). At the same time the upper jaw must be able to open and close quickly and with minimum muscular force especially when closing the jaws rapidly when a fish slides up the blade of the lower jaw. Although the two different types of secondary articulations can be shown to be survival features in birds possessing them, they are adaptations to quite different selective agents depending on the exact method of feeding by the species of bird.

(f) Sunbathing in African vultures

Many birds sunbath although this behavior has been shown to be different adaptations in diverse groups. In the roadrunners of North America (*Geococcyx*; Cuculidae), sunbathing serves to obtain additional heat from solar radiation (Ohmart and Lasiewski 1971). In cormorants (*Phalacrocorax*; Phalacrocoracidae), sunbathing dries the feathers after the bird has completed swimming and diving for food; these birds do not have water-proof feathers. Some species of Old World griffon vultures (*Gyps*; Accipitridae) sunbath, but during the heat of the day when one would expect that these birds would want to cool off rather than acquiring additional heat (Houston, 1980). Careful observations and tests showed that sunbathing behavior in these birds serves to straighten by means of solar heat their large flight feathers which have become bent upwards during a long period of soaring while looking for food. Sunbathing in diverse birds has a number of different functions and serves as a survival feature to diverse selective agents.

(g) Dodos and seed coats

Until about 1665, dodos (*Raphus cucullatus*; Columbiformes: Raphidae) lived on the island of Mauritius east of Madagascar in the western Indian Ocean; they are the symbol of extinction with the English expression being 'Dead as a dodo.' Dodos apparently lived largely on fruits and seeds, including the fleshy fruit of the tambalacoque tree (*Siderox-*

ylon grandiflorum [cited as *Culvaria major* by Temple]; Sapotaceae). The seeds within the outer pulp of this fruit have a very hard shell, preventing germination when entire; the seed coat has to be cracked in some way to permit water to enter the seed and activate germination. There are a few young specimens of this tree species on the island (Gibbs, *et al.*, 2001:172–3) but most of these trees are mature individuals still fruiting abundantly. Tests showed that the seeds would germinate normally if cracked carefully with a hammer, or if fed to turkeys (*Meleagris gallopavo*) and passed through their digestive track (Temple, 1977). Grinding of the seeds by the heavily muscular stomach of the dodo (or of the alien turkey) is apparently sufficient to crack the thick seed coat. It can be argued that the thick coat of these seeds is a reproductive feature that permitted the seeds to pass through the digestive system of the dodo without the seed being destroyed, but cracked just enough so that germination can occur after the seed is voided. This system permits dispersal of the seeds of this tree away from the parent tree. It is not clear whether the thick seed coat in the tambalacoque tree could also be considered as a survival feature (associated with dispersal of seeds) or just a direct reproductive feature (survival of the offspring - seed - of the adult tree when passing through the digestive system of the dodo).

ORIGIN OF SURVIVAL AND REPRODUCTIVE FEATURES

Once a survival or reproductive feature has been determined in an organism, the next and separate question is how this attribute came into being. A particular adaptation, be it a survival or a reproductive feature, does not have to evolve under the action of the same selective agent to which it is now associated, but could have evolved under the action of other selective agents or have originated because it is linked pleiotropically with the evolution of other attributes. The determination of particular survival and reproductive features is generally a daunting task, but ascertaining the actual process of adaptation evolution of existing features is much more difficult or impossible because these are historical-narrative explanations. It is simply not possible in almost all cases to know the detailed environmental factors and selective agents acting on the organism except for very short times spans back from the present. These causes and the initial plus boundary conditions are essential for successful historical-narrative explanations (Bock, 2000) and can rarely be even guessed with accuracy.

Under the demands placed by Gould and Vrba (1982) for the assessment of adaptations, the number of biological attributes that can be actually labeled as adaptations would be varnishing small because it is generally impossible to determine whether a particular feature evolved under the action of the same selective agent to which it is now associated. This is the major reason why the concept of exaptation is without usefulness in nomological evolutionary theory.

SYSTEMATIC INVESTIGATION

Herein, I am interested in the role of functional/adaptive analyses in historical-narrative explanations such as evolutionary history of groups, classifications, and Haeckelian phylogeny (Mayr and Bock, 2002). The importance of ecological aspects in animal and plant systematics at the specific level had been discussed respectively by Selander (1969) and Kruckeberg (1969). To be scientific, historical evolutionary explanations must be based on well tested nomological explanations (Szalay and Bock, 1991). In addition these historical explanations are most difficult because many or most initial and boundary conditions are not known (Bock, 1999, 2000). Often it is not possible to choose between several to many reasonable historical evolutionary explanations and the choice becomes rapidly difficult or impossible as the explanation becomes more specific. Virtually no doubt exists for the conclusion that birds originated from reptiles, and little doubt for the claim that birds arose from the Archosauria. But there is still great difficulty, at best, in choosing between whether birds evolved from a primitive archosaur, such as the basal Thecodontia, or from a saurischian dinosaur (e.g., Dromaeosauridae: Theropoda). Are the New World Vultures (Cathartidae) members of the Falconiformes or the Ciconiiformes (close to the storks: Ciconiidae)? How does one classify the many forms of warblers, flycatchers, shrikes, and finches within the Oscines (Passeriformes)? The goal is not just to offer historical evolutionary explanations that are supported by the available evidence, but to provide *strongly convincing* explanations.

When faced with such problems, evolutionary biologists and systematists have almost always advocated two approaches. The first is to add ever more morphological features to the analysis (with the realization that almost all evolutionary and systematic studies are still done using comparative investigations of morphology), and preferably using as many such features as possible as is been done in phenetics (numerical taxonomy) and during the last two decades in numerical cladistics. Parsimony analysis, as universally used in these methods, does not solve the problem because there is no evidence that evolutionary change always proceeds in a parsimonious manner. Parsimony is invoked only because of the computer algorithms used; otherwise an exceedingly large number of solutions would result. Even with the use of parsimony most numerical cladistic investigations results in a large number of 'equally parsimonious' trees, with little said on how one is chosen from the many. The other approach is to employ different types of characters, most recently either biochemical characters or DNA sequences. Neither approach has provided a full solution, largely because both still share the fundamental shortcoming of traditional comparative morphological analyses which is to elucidate historical evolutionary explanations using only a comparison of form (= structural philosophy). Yet from an understanding of nomological evolutionary the-

ory, it is not possible to provide convincing historical evolutionary explanations without the inclusion of functional and adaptive assessments of the phenotypic attributes used in the analysis. Form alone is not adequate contrary to the theses of structural philosophy.

The conclusion that addition of more characters will provide greater support of a historical evolutionary hypothesis is based on a simple statistical argument that a large number of characters will provide enough true homologues to test the group hypothesis. Further it is assumed that the homoplastic attributes will cancel out one another. But these assumptions depend on how well the individual homologous have been tested and examined for their degree of confidence (Bock, 1989) - matters that have scarcely been considered by most systematists.

After concluding that features in different organisms are homologous, it is necessary to determine the degree of confidence of this conclusion. This confidence can vary from low to high although precise values of the different degrees confidence cannot be given. Assignment of the degree of confidence requires additional study and is basically an assessment of whether the feature evolved only once, or twice to many times. A low degree of confidence in a particular homologous feature have does not affect the earlier conclusion about their homology — these features may still be homologous, but they are of little to no value in testing group hypotheses. Only homologous features possessing a high degree of confidence are useful in tests of group hypotheses. Assessing the degree of confidence of character hypotheses (both homology and plesiomorphic-apomorphic relationships) ought to include functional/adaptive analyses as these are necessary for understanding the possible evolutionary history of the features.

The search for useful features in the structure of proteins and the sequence of nucleotides in DNA is based on the widespread, but tacit belief of most systematists that attributes ever closer to the beginning of ontogenetic development would have increasing importance in supporting group hypotheses; proteins and DNA sequences constituting the apex of such importance. The use of these features cannot be gainsaid, but little is still understood on how proteins and nucleotide sequences evolve as well as their relationship to selective agents acting on organisms.

As alluded above, the approach that has the greatest promise to provide support and confidence for historical evolutionary explanations is carefully done functional/adaptive analyses of the attributes used in the character hypotheses. This method requires a deep understanding of the functional properties of the taxonomic features used and of their possible ecological relationships, in addition to careful comparison of the properties of form, all of which requires considerable knowledge and work. A few examples will demonstrate the value of such studies; others can be found in my earlier papers (Bock, 1969, 1992).

(a) Palaeognathous birds

The relationships and biogeography of the flightless

ratite birds and the flying neotropical tinamous had been an enigma for over 100 years ever since Huxley (1867) described the different types of bony palate in the avian skull. By the 1950s, most ornithologists concluded that the so-called palaeognathous birds were not related to one another because of their disjunct distribution in the southern continents. In 1960 I undertook a comparative study of the entire skull of these birds (Bock, 1963) and demonstrated the existence of a series of functionally interrelated cranial features that are correlated with the palaeognathous palate. This homologous complex of features supports the monophyly of the palaeognathous birds within the Aves; this conclusion was quickly accepted and was subsequently substantiated by other characters, including biochemical ones and DNA sequences. Virtually all workers still placed the flying tinamous of the Neotropics as a separate taxon from the large, flightless ratites, as well as considering the African ostrich and South American rheas to be sister groups within the flightless ratites. In a subsequent study of the complex tongue apparatus, we found (Bock and Bühler, 1990) that the anterior bones and tongue muscles of the ostrich to be strikingly different from those found in the rheas and tinamous. The rheas and tinamous have a narrow rod-like basihyle articulating to the plate-like fused paraglossalia by means of a massive *M. hypoglossus obliquus*. The muscular articulation between bones as seen in these birds is unique in birds and perhaps in vertebrates. In the ostrich, the basihyle is broad and flat and articulates at its anterolateral corners with the long, thin, splint-like, unfused paraglossalia. Significant is the completely absent *M. hypoglossus obliquus* in the ostrich which demonstrates that rheas and tinamous could not have descended from ostriches because vertebrate striated skeletal muscles do not originate *de novo*. Skeletal muscles originate only by budding from existing muscles, and the lack of this muscle in ostriches precludes it being ancestral to the rheas and tinamous. Although the palaeognathous birds are monophyletic, the large flightless ratites are not monophyletic within the palaeognaths; further the tinamous and rheas constitute a monophyletic group that possibly includes the Australasian ratites. This conclusion is at variance with those reached on the basis of the comparisons made with other morphological features and DNA sequences; these studies are difficult to evaluate because they do not include functional-adaptive analyses of the compared attributes.

(b) Oscine finch groups

Adaptive radiation in the song birds (Passeriformes: Oscines) has resulted in a number of genera sharing the same feeding specialization, such as warblers, flycatchers, shrikes and seed-eating finches, which have often been placed in the same family-level taxon. Unraveling of these 'scrap-basket groups' has been a major problem because of the great similarity of all song birds; most of this work must still be completed. Useful clues to analyze the possible relationships of seed-eating Oscines can be found in the complex of features of the structures used to shell seeds before

swallowing them (Ziswiler, 1965, 1967, 1980). A component of this morphological complex is the corneous tongue serving as a 'seed cup' to position and hold seeds in place as the seed-coat is removed (Bock and Morony, 1978a, b). The suggestion of the taxonomic usefulness of this feature came from the discovery in *Passer* of a heterotropic skeletal neomorph, the preglossale bone, which is associated with the enlarged paired *M. hypoglossus anterior* (absent in other seed-eating finches). These features are not found in any other oscine finch and serves to separate the passerine finches as a monophyletic taxon from the Ploceidae in which they have been placed by most workers; further the passerine finches are not closely related to any of the other groups of seed-eating oscines. Structure of the seed-cup also suggests that the Ploceidae, the Estrildidae and the Fringillidae + Emberizidae have also evolved their seed eating habits independently of one another and of the Passeridae.

CONCLUSIONS

Both sets of examples demonstrate without any doubt that credible and persuasive evolutionary explanations, both nomological and historical, are not possible in the absence of careful examination of the interactions between the phenotype and selective agents arising from the external environment. Both types of explanations depend on thorough functional/adaptive analyses, and as such require work in the laboratory and in the field, especially for the empirical testing of diverse character hypotheses and determination of their degree of confidence. This is especially true for historical evolutionary explanations, such as classifications and phylogenies, which have gyrated wildly during the past several decades in spite of the development of new approaches, search for new characters and computer methods, and the large amount of effort put into macrosystematics. After some 150 years since the publication of Darwin's *On the origin of Species* in which biological classification was finally placed on an empirically testable scientific nomological-deductive basis, the time has come to insist that these historical evolutionary studies be placed firmly and fully on nomological evolutionary theory and especially on the essential functional-environmental-adaptive investigations. Otherwise, to use an American expression, we will simply continue to spin our wheels and get nowhere fast.

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