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Origin versus existence of adaptive features

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Summary: The concept that many or most features of organisms are adapted to environmental demands placed on the organisms predated Darwin's formulation of evolutionary theory; his contribution was to provide a scientific explanation for these adaptations and their origins. Because the term adaptation is used for both the process and the state of being, confusion has existed ever since 1859 on the meaning and scope of adaptation, as well as the biological units that can be considered to be adaptations. Adaptations should be restricted to phenotypical attributes of organisms; they form the components of fitness of the individual organisms and include survival features, direct reproduction features and indirect reproduction features. Adaptations are judged relative to the demands of selective agents arising from the external environment, not simply to environmental factors, acting on the organism. Elucidation of adaptations as the state of being are nomological-deductive explanations within evolutionary theory. A phenotypic feature could be adapted simultaneously to two or more selective agents. Further it could be a survival feature to quite different selective demands, and/or a direct or an indirect reproductive feature. Once a feature is shown to be an adaptation, the next question to ask is its evolutionary origin which is a historical-narrative explanation and which is far more difficult to answer. In general, it is impossible to show that a feature evolved adaptively with the same selective agent to which it is now adapted. Exaptation is an unnecessary term in evolutionary theory as almost always no way exists, almost always, to distinguish between exaptations and non-exaptations. Care must be taken in the analysis of features to insure whether one is considering the existence of an adaptation, the origin of the adaptation, whether the adaptation is a survival or a reproductive feature or both, and the possible multiple adaptiveness of the attribute in the same or diverse organisms.

Key words: Evolution, fitness, adaptation, survival features, reproductive features

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Introduction: With the introduction of evolutionary thinking into biology by DARWIN in 1859, biological morphologists were faced with an entirely new set of questions about the features they studied. This question was not whether these features were adaptations to demands of the external environment because this concept was well established at least since 1800. The important question was how did these adapted features come into being, with the distinction between an adaptation as a state of being and adaptation as a process over evolutionary time. Little attention was given to this distinction which remains a much debated question to the present time. I would like to inquire into the difference between the existence of adaptations and their origins in this paper dedicated to my close friend and colleague PAUL BÜHLER who was an outstanding teacher and avian evolutionary morphologist and who thought deeply about these and other matters in morphology and evolutionary biology.

The questions to be considered are:

a) What is an adaptation and what are the components of fitness? These are nomological-deductive explanations.

b) What is adaptive evolutionary change and what are the possible evolutionary origins of adaptations? These are historical-narrative explanations.

c) Is the concept of exaptation necessary is addition to the concept of adaptation in either nomological or historical evolutionary biology? This is largely, but not exclusively a nomological-deductive explanation.

Explanations in Science: Concepts about explanations in science are based almost inclusively on chemistry and physics; but these sciences have been delimited by their practitioners to a strictly nonhistorical endeavor. Hence the scope of admissible scientific explanations advocated by philosophers of science is limited almost exclusively to nomological-deductive ones which is inadequate for any science, such as biology and geology, containing a historical component (BOCK, 2000). For these sciences with a historical component, an additional form of explanation — the historical-narrative — is also required. These historical-narrative explanations are (a) historical in nature in that means that earlier events affect later ones, (b) deal with singular events rather than with universals, (c) have a probability of being correct, and (d) must be stated carefully with special attention given to the associated initial and boundary conditions (frequently referred to vaguely as "constraints," see GOULD & LEWONTIN 1979). Most importantly, in order to be scientific, a historical-narrative explanation must be based firmly on pertinent and well tested nomological-deductive explanations which together with the objective empirical observations, form the chain of arguments used in testing the particular historical-narrative explanation. Without this foundation of pertinent nomological-deductive explanations, historical-narrative explanations would fall outside of science proper. The vague and scientifically undefined term "scenario" has often been used in a derogatory sense for historical-narrative explanations and may be equivalent to historical-narrative explanations lacking a nomological-deductive core.

With these two types of explanation in mind, any science with a historical component must be considered to have nomological theories and historical theories, the latter always depending on the former. Within biology, one must speak of nomological evolutionary theory and historical evolutionary theory (Bock 2003). Full clarity in biology, not only evolutionary biology. is dependent on proper distinction between these two types of evolutionary theory.

Nomological evolutionary theory includes all causes and mechanisms of evolutionary change such as speciation and phyletic evolutionary change, elucidation of the adaptiveness of attributes of organisms, fitness of individual organisms, causes and mechanisms of genetics, dispersal abilities of individuals, interactions of individuals with the external environment and with selective agents, and all concepts such as the species concept, the niche concept, etc. Historical evolutionary theory includes the elucidation of the evolutionary history (= phylogeny) of groups of organisms and of their attributes, historical biogeography and any other part of biology dealing with the history of living organisms and their world.

Adaptation: Unfortunately the terms "adaptation, adaptive, adapted," and etc. have acquired a very broad and generally vague meaning within evolutionary writing and have been used in a diversity of ways and at a diversity of biological levels. Genes, phenotypic attributes, organisms, species, ecosystems, sex ratios, and mutations have all be termed adaptive without any specification of what is meant by this designation. Use of the term "adaptive" for evolutionary changes designates those modifications brought about by the action of selective agents, hence Darwinian evolution, in contract to non-adaptive or non-Darwinian evolution. Because selective agents arising from the external environment act on the organism and not on the individual features of the organism, it must be emphasized that equating adaptive evolution with Darwinian evolution applies most correctly to evolutionary change when considering the whole organism, but not always when considering the evolution of individual attributes of organisms, such as the evolution of the mammalian jaw articulation. Because of the numerous pleiotrophic associations between diverse attributes of organisms, the observed or inferred evolutionary change in a particular trait may not be adaptive, but occurred because of adaptive change in some other trait. This holds even if the evolution of populations of whole organisms is clearly adaptive. Care must be taken in discussing adaptive evolutionary change in the entire organism (always as a population phenomenon) as contrasted to discussing adaptive evolutionary change in individual features of organisms because what is true for the former may not be true for the latter. And almost all discussions about evolutionary change are presented in terms of individual traits, not for the entire organism.

Adaptation has also been used in an overly broad fashion, being applied to genes, the genotype, phenotypic features of organisms, the niche, etc., but only phenotypic attributes of organisms should be considered as adaptations. Further, adaptation has been generally only for "survival features" (BOCK & VON WAHLERT 1965) which is too narrow a usage. Adaptations also include both direct and indirect reproductive features (BOCK 1993, 2002), which together with survival features, constitute (all?) components of fitness of the individual. As such an adaptation can be defined as: *any phenotypic feature of an individual organism which statistically increases the fitness of that individual relative to other individuals in the population* (BOCK 2003 282). Fitness in nomological evolutionary theory since 1930 has been defined as: *the contribution of an individual to the gene pool of the next (or some future) population.* Fitness should always be considered in terms of inclusive fitness, and best as that inclusive fitness in which the individual has an active role. To have a positive fitness an individual must have both survival and reproductive features. 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 adapted attributes to a greater number of individuals in the next generation if these traits are, at least in part, heritable. Fitness of an individual can be measured relatively easily by counting numbers of its direct and collateral offspring, 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 survival feature (BOCK, 2003:283) can be defined as: *a phenotypic attribute of an organism having properties of form and function which permit the organism to interact successfully (= continued survival of that organism) with the demands of the selective agents of the external environment of that organism and with a certain degree of efficiency.* Survival features are what biologists have generally consider to be adaptations (e.g., BOCK & VON WAHLERT 1965), but survival features are not the only component of the fitness of individual organisms which depends on the combination of their survival and their reproduction.

The other components of fitness are direct reproductive features (for the production of direct offspring) and indirect reproduction features (for the production of collateral offspring; sometimes called kin selection; but see BROWN 1987); these reproductive features include but are not synonymous with features 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 phenotypic feature of an organism having properties of form and function which permit the organism to produce direct offspring (= descendent kin) successfully under the demands of the selective agents of the external environment of that organism and with a certain degree of efficiency* 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.

Almost all well developed features of organisms are adaptations, but determining whether a particular phenotypic feature in an organism is an adaptation is generally a most difficult task contrary to the conclusions of GOULD & LEWONTIN (1979). Such work must begin with careful descriptions of the properties of form and of function of the feature, and continue with observations of how the organism uses the feature in its normal environment either for survival or reproduction or both. The latter observations are essential as it is not possible to ascertain the adaptiveness of a feature in the absence of studying the organism in its natural environment. Comparisons of the properties of form, and even function, in different organisms are not sufficient to reach conclusions about the adaptiveness of a feature (BOCK 1967). Hence it is not possible to reach conclusive answers about the adaptiveness of features in fossil organisms and all Recent organisms which cannot be observed directly in their normal environment. For many or most Recent organisms, such observations are difficult or not possible.

Some well-developed features are not adaptations, generally because they have lost their adaptiveness due to the disappearance of the selective agent to which they have formally been adaptive. One possible example is the relationship between the now extinct Dodos (*Raphus cucullatus*; Mauritius, West Mascarene Islands) and the fruit of the native tambalacoque tree (TEMPLE 1977; but see WITMER & CHEKE 1991 for an opposing viewpoint – this great difference of opinion shows the problems in historical evolutionary explanations which is the heart of this particular dispute). Dodos apparently lived largely on fruits and seeds, including the fleshy fruit of the tambalacoque tree (*Sideroxylon grandiflorum*; Sapotaceae). The seeds within the outer pulp of this fruit have a very hard shell, often preventing germination when it is entire; the seed coat generally 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 tambalacoque tree seeds by the heavily muscular stomach of the dodo (or by that 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 an 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.

The best, and perhaps the only suitable research program to determine whether a feature is or is not an adaptation is the "adaptationist program," again contrary to the conclusions of GOULD & LEWONTIN (1979). This research program is based on nomological evolutionary theory and is formulated on the assumption that all features of organisms are adaptations, unless shown otherwise. It does not provide an answer to the exact nature of the adaptiveness of individual phenotypic attributes or the selective agent to which they are adapted. One has to work very hard with a real understanding of the properties of the feature and of the possible selective agents to show the adaptiveness of a feature. If after much effort to determine the adaptiveness of the feature is without success, then one has the possibility to conclude that this trait in this organism is not an adaptation. And in many, or most cases, some real insight into the organism and its relationships to its external environment is necessary. One cannot give up ascertaining the adaptiveness of a features after a few attempts as implied by Gould and Lewontin. And one must remember that the same trait in different organisms might be diverse adaptations to a quite different selective agent. In some cases the same feature might be a survival feature in some organisms and a reproductive feature in others, or possibly both a survival and a reproductive trait in still other organisms.

A good example of the diversity of the adaptiveness of the same feature in different organisms is seen in the intramandibular hinge in the lower jaw of birds as nicely discussed by PAUL BÜHLER (1970, 1981) in the Eurasian Nightjar (*Caprimulgus europaeus*). This feature is 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. 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 or to form a larger trap to catch insects, 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 and pelicans, 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 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, a survival feature in other groups to quite different selective agents and might be both in still others. The exact nature of the adaptiveness and the associated selective agents have to be established separately for each individual case.

Another example is enlarged mucus-secreting glands 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 (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.

Origin of Adaptations: A definite distinction must be made between the origin of phenotypic traits of organisms and the origin of the adaptiveness of these traits, recalling that evolutionary change depends on the simultaneous action of two different set of causes – the one associated with the origin of new phenotypical variation in a population of organisms and the second associated with the action of selective agents on these individual organisms. It is of real interest to know whether a new feature (or a major modification in an existing feature) arose evolutionarily because of a change in the genes directly affecting that feature, or because of selection for one trait (albinism) that also brings about changes in other traits (such as deafness and lack of adrenaline in albino tigers because the normal traits depend on proper development of the neural crest cells; selection was for albinism which appeared because of arrested migration of the neural crest cells which also affected negatively proper development of the bones of the middle ear and the cortex of the adrenaline gland), or because of structural/ functional interactions between features in the body (such as the formation of articulations when two bones move against one another), or other types of pleiotrophic interactions.

As an example, the mammalian jaw articulation is a new feature in the history of the vertebrates and it appeared as a consequence of the enlarging coronoid process of the mandibular ramus rubbing against the squamosal bone of the braincase. When this new dentary-squamosal articulation first appeared, it was because of the consequences of the mechanical interactions of the two bones – a case of physiological adaptation or somatic interactions (see Bock 2000). The mammalian articulation has appeared as a new feature through the mechanisms of physiological adaptation whenever the two bones rubbed together over a long period in the life of an individual, but only as an adaptation when individuals possessing this new articulation were favored by selective agents different from those responsible for the enlargement of the coronoid process. The advantage gained is associated with improved action of the jaw apparatus with the direct articulation of the lower jaw with the brain case compared with having a moveable quadrate bone intervening between the lower jaw and the braincase.

Hence the distinction must be made between the question of the origin of a feature and the origin of the adaptiveness of this feature; both are of interest, but they are different questions. Herein, I am interested in the origins of adaptations, having defined and recognized individual phenotypic features as adaptation within nomological evolutionary theory.

Noting the distinction between nomological and historical evolutionary theory, the proper procedure is to ascertain first whether a particular phenotypic feature is or is not an adaptation and then to determine how that adapted feature evolved. It is clearly not proper to include in the definition of adaptation a historical criterion as does Gould and VRBA (1982) which confuses completely the distinction between nomological evolutionary theory and historical evolutionary theory. A feature is an adaptation with respect to a particular selective agent acting on the organism regardless of how this feature evolved. This is similar to the observation that water is water regardless of whether it came into being by the combustion of hydrogen in the presence of oxygen or by the decomposition of hydrogen peroxide into water and oxygen.

As any other historical explanation in evolution, elucidation of the evolutionary history of any adaptation is exceedingly difficult, if not impossible because of the generally complete lack of any factual knowledge of the ecological relationships of the organisms during earlier times and of the selective agents acting on them during the origin and evolutionary history of the attribute. Even if it is possible to deduct the selective agents acting during the evolution of a particular feature, it may not be possible to elucidate the exact sequence of their action which is essential for a historical explanation. Features that can be shown to be an adaptation to a particular selective agent at present could have evolved under the action of that selective agent, or under the action of some different selective agent, or because of a pleiotrophic connection with some other feature of the organisms evolving under the control of a completely different selective agent.

Perhaps the only generalization that can be offered is that in the origin and evolution of most (or almost all) features they pass through one or more preadapted stages and are therefore acted on by more than one selective agents during their evolution (BOCK 1959; = Functionswechsel, DOHRN 1875).

Because of the extreme, if not impossible, difficulty of elucidating the evolutionary history of adapted attributes of organisms, the distinction claimed by Gould and VRBA (1982) between adaptations and exaptations has no justification. Adaptations for Gould and VRBA are features that evolved under the action of the same selective agents to which they are currently adapted. Exapations are those features that have not evolved under the action of the selection agents to which they are now adapted.

First, their definitions of these two terms confuse nomological and historical evolutionary theories; the definition of and the recognition of particular features as adaptations is strictly a part of nomological evolutionary theory. Gould and Vrba define adaptation and exaptation historically, that is, in terms of their past evolutionary history. Second, even if one accepts their definitions, then for almost all features of Recent organisms, no way exists on which to decide whether these features are adaptations or exaptations because of the virtual impossibility of knowing their evolutionary history with the precision needed. If it is not possible to separate objects in science into two or more different categories, such as adaptations and exaptations in the sense of Gould and Vrba, then those concepts are of no value and should be discarded even if they are defined validly.

Avian feathers are an excellent example of this problem as feathers found in Recent birds not only belong to a number of different morphological types (not necessarily always sharply distinct from one another), but have a number of dissimilar functions and biological roles so that various avian feathers types can be shown to be diverse adaptations to (a) provide life and thrust in flight (wing and tail feathers) (b) streamlining as shown excellently by Paul Bühler (1990) for the neck feathers of owls and generalized by Homberger (2002) for contour feathers, (c) insulation (contour feathers), (d) specialized mechanoreceptors (bristles around the mouth in many insect-eating birds), (e) protective coloration, (f) courtship coloration and specialized plumes, (g) sound production (*Scolopax*, *Gallinago*) (h) waterproofing, (i) carrying water for young (in the Pteroclididae), among other possible adaptations. Clearly some of these feather types and their adaptiveness (sound production and water carrying) are derived, having evolved after other feather types had appeared, but this does not solve the question of the original appearance of avian feathers. Different workers have postulated that avian feathers evolved originally with respect to flight (providing the necessary power), insulation, streamlining of the body for flight, mechanorecptors as well as other less probable historical explanations. Hence, if one examined avian feathers in general, or a particular type of feather, or the association of flight feathers or contour feathers with diverse biological roles and selective agents such as flight + courtship display + sound production for flight feathers or insulation+protective coloration + courtship display + streamlining of the body for contour feathers, it would be impossible to say whether avian feathers or a particular type of avian feathers would be an adaptation or would be an exaptation in the sense of Gould and Vrba. It makes much more sense to examine different feather types and to determine their diverse possible adaptiveness with respect to various selective agents (nomological evolutionary theory) and then to start working on the very difficult historical explanation of how feathers arose and how the many diverse adaptive properties of avian feathers evolved thereafter.

Concluding Remarks: Contrary to common belief, the major advances in science do not come from the discovery of new facts, but from the clarification of concepts with their associated terminology and the elucidation of theories and their systems of explanations. Biology and especially evolutionary biology has been seriously remiss in these two fundamental areas of theory. Terms are used in a sloppy and vague fashion. And there has been an almost complete lack of interest in explanatory systems. These difficulties exist in an almost classic way for the concept of adaptation within evolutionary biology. Part of this problem, and I should emphasized that it is only part of the problem, is that the areas of evolutionary morphology and nomological macroevolutionary theory have not contributed much, if anything, to the Evolutionary Synthesis (MAYR & PROVINE 1980). As is well known, morphology declined in importance and in its contributions to biology since the start of the 20th century and had reached a low point by the period of the evolutionary synthesis. Prior to 1900, the contribution of comparative morphology had been almost exclusively to historical evolutionary theory, such as forming a major foundation for the classification and phylogeny of organisms. The newer approaches of functional and ecological morphology had to develop before this classical field could contribute significantly to nomological evolutionary theory. And these advances began strongly only well into the 1950's after the end of the generally accepted period of the synthesis (1937 - 1950). Although they form a small minority among vertebrate morphologists and although a famous comparative anatomist has expressed the opinion that: "To the student of habits, songs and plumage, the birds have much to offer· they offer little, however, to those interested in anatomic structure and function." avian morphologists, including PAUL BÜHLER, have contributed disproportionally strongly to understanding such nomological concepts such as adaptation and major evolutionary change and their application to historical evolutionary theory.

Zusammenfassung

Ursprung und Existenz adaptiver Eigenschaften. Das Verständnis dafür, dass viele oder die meisten Eigenschaften von Lebewesen den Anforderungen entsprechen, die Umwelt und Umgebung ihnen stellen, ist älter als Darwins Formulierung der Evolutionstheorie; sein Beitrag war, für Anpassungen und ihre Entstehung einen wissenschaftlichen Beweis zu liefern. Weil der Begriff Anpassung sowohl für den Vorgang wie den Zustand gebraucht wird, hat seit 1859 Verwirrung über Bedeutung und Umfang von Anpassung geherrscht. Der Gebrauch des Begriffs „Anpassung" sollte auf die phänotypischen Merkmale von Organismen beschränkt sein; sie bilden die Elemente der Fitness des Einzelorganismus und umfassen Eigenschaften für das Überleben sowie solche von direkter wie indirekter Bedeutung für die Fortpflanzung. Anpassungen werden im Hinblick auf Anforderungen der Auslesekräfte beurteilt, die von der (äußeren) Umgebung ausgehen und auf die Organismen einwirken, nicht einfach im Hinblick auf

die ökologischen Faktoren selbst. Innerhalb der Theoriebildung ist die Aufklärung einer Anpassung als Zustand, methodisch gesehen, ein nomologisch-deduktives Vorgehen. Eine phänotypische Eigenschaft kann gleichzeitig zwei oder mehr Selektionskräften gerecht werden. Sie könnte ferner gleichzeitig in mehr als einer Hinsicht überlebenswichtig, und/oder von direkter oder indirekter Bedeutung für die Fortpflanzung sein.

Wenn eine Eigenschaft als Anpassung nachgewiesen ist, stellt sich als nächste Frage die nach ihrer Entstehung in der Evolution; das ist eine historisch-narrative Frage, und sie ist weit schwieriger zu beantworten. Gewöhnlich ist der Nachweis unmöglich, dass eine Eigenschaft unter den gleichen Selektionsbedingung adaptiv geworden ist, denen sie jetzt gerecht wird. „Exaptation“ ist aber in der Theorie der Evolution ein unnötiger Begriff, da es fast keine Möglichkeit gibt, „Exaptationen“ von „Nicht-Exaptationen“ zu unterscheiden.

Bei dieser Untersuchung von Eigenschaften muss mit aller Sorgfalt deutlich gemacht werden, ob sie dem Vorliegen einer Anpassung oder der Genese einer Anpassung gilt, ob die Anpassung dem Überleben oder der Fortpflanzung oder aber beidem dient, und ob etwa möglicherweise eine multiple Anpassung des Merkmals im gleichen oder in verschiedenen Organismen vorliegt.

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