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Exaptation—a missing term in the science of form

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Abstract.—Adaptation has been defined and recognized by two different criteria: historical genesis (features built by natural selection for their present role) and current utility (features now enhancing fitness no matter how they arose). Biologists have often failed to recognize the potential confusion between these different definitions because we have tended to view natural selection as so dominant among evolutionary mechanisms that historical process and current product become one. Yet if many features of organisms are non-adapted, but available for useful cooptation in descendants, then an important concept has no name in our lexicon (and unnamed ideas generally remain unconsidered): features that now enhance fitness but were not built by natural selection for their current role. We propose that such features be called *exaptations* and that adaptation be restricted, as Darwin suggested, to features built by selection for their current role. We present several examples of exaptation, indicating where a failure to conceptualize such an idea limited the range of hypotheses previously available. We explore several consequences of exaptation and propose a terminological solution to the problem of preadaptation.

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I. Introduction

We wish to propose a term for a missing item in the taxonomy of evolutionary morphology. Terms in themselves are trivial, but taxonomies revised for a different ordering of thought are not without interest. Taxonomies are not neutral or arbitrary hat-racks for a set of unvarying concepts; they reflect (or even create) different theories about the structure of the world. As Michel Foucault has shown in several elegant books (1965 and 1970, for example), when you know why people classify in a certain way, you understand how they think.

Successive taxonomies are the fossil traces of substantial changes in human culture. In the mid 17th century, madmen were confined in institutions along with the indigent and unemployed, thus ending a long tradition of exile or toleration for the insane. But what is the common ground for a taxonomy that mixes the mad with the unemployed—an arrangement that strikes us as absurd. The "key character" for the "higher taxon," Foucault argues, was idleness, the cardinal sin and danger in an age on the brink of universal commerce and industry (Foucault's interpretation has been challenged by British historian of science Roy Porter, MS). In other systems of thought, what seems peripheral to us becomes central, and distinctions essential to us do not matter (whether idleness is internally inevitable, as in insanity, or externally imposed, as in unemployment).

II. Two Meanings of Adaptation

In the vernacular, and in sciences other than evolutionary biology, the word adaptation has several meanings all consistent with the etymology of *ad* + *aptus*, or towards a fit (for a particular role). When we adapt a tool for a new role, we change its design consciously so that it will work well in its appointed task. When creationists before Darwin spoke of adaptation—for the term long precedes evolutionary thought—they referred to God's intelligent action in designing organisms *for* definite roles. When physiologists claim that larger lungs of Andean mountain peoples are adapted to local climates, they specify directed change for better function. In short, all these meanings refer to historical processes of change or creation for definite functions. The "adaptation" is designed specifically for the task it performs.

In evolutionary biology, however, we en-

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* An equal time production; order of authorship was determined by a transoceanic coin flip.

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TABLE 1. A taxonomy of fitness.

Process	Character		Usage
Natural selection shapes the character for a current use—adaptation	adaptation	aptation	function
A character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use—cooptation	exaptation		effect
A character whose origin cannot be ascribed to the direct action of natural selection (a nonaptation), is coopted for a current use—cooptation			

counter two different meanings—and a possible conflation of concepts—for features called adaptations. The first is consistent with the vernacular usages cited above: a feature is an adaptation only if it was built by natural selection for the function it now performs. The second defines adaptation in a static, or immediate way as any feature that enhances current fitness, regardless of its historical origin. (As a further confusion, adaptation refers both to a process and a state of being. We are only discussing state of being here—that is, features contributing to fitness. We include some comments about this further problem in section VIE.)

Williams, in his classic book on adaptation, recognized this dilemma and restricted the term to its first, or narrower, meaning. We should speak of adaptation, he argues, only when we can "attribute the origin and perfection of this design to a long period of selection for effectiveness in this particular role" (1966, p. 6). In his terminology, "function" refers only to the operation of adaptations. Williams further argues that we must distinguish adaptations and their functions from fortuitous effects. He uses "effect" in its vernacular sense—something caused or produced, a result or consequence. Williams' concept of "effect" may be applied to a character, or to its usage, or to a potential (or process), arising as a consequence of true adaptation. Fortuitous effect always connotes a consequence following "accidentally," and not arising directly from construction by natural selection. Others have adopted various aspects of this terminology for "effects" *sensu* Williams (Paterson 1981; Vrba 1980; Lambert, MS). However, Williams and others usually invoke the term 'effect' to designate the *operation* of a useful character *not* built by selection for its current role—and we shall follow this restriction here (Table 1). Williams also recognizes that much haggling about adaptation has been "encouraged by imperfections of terminology" (1966, p. 8), a situation that we hope to alleviate slightly.

Bock, on the other hand, champions the second, or broader, meaning in the other most widely-cited analysis of adaptation from the 1960's (Bock and von Wahlert 1965; Bock 1967, 1979, 1980). "An adaptation is, thus, a feature of the organism, which interacts operationally with some factor of its environment so that the individual survives and reproduces" (1979, p. 39).

The dilemma of subsuming different criteria of historical genesis and current utility under a single term may be illustrated with a neglected example from a famous source. In his chapter devoted to "difficulties on theory," Darwin wrote (1859, p. 197):

> The sutures in the skulls of young mammals have been advanced as a beautiful adaptation for aiding parturition, and no doubt they facilitate, or may be indispensable for this act; but as sutures occur in the skulls of young birds and reptiles, which have only to escape from a broken egg, we may infer that this structure has arisen from the laws of growth, and has been taken advantage of in the parturition of the higher animals.

Darwin asserts the utility, indeed the necessity, of unfused sutures but explicitly declines to label them an adaptation because they were not built by selection to function as they now do in mammals. Williams follows Darwin and would decline to call this feature an adaptation; he would designate its role in aiding the survival of mammals as a fortuitous effect. But Bock would call the sutures and the timing of their fusion an adaptation, and a vital one at that.

As an example of unrecognized confusion, consider this definition of adaptation from a biological dictionary (Abercrombie et al. 1951, p. 10): "Any characteristic of living organisms which, in the environment they inhabit, improves their chances of survival and ultimately leaving descendants, in comparison with the chances of similar organisms without the characteristic; natural selection therefore tends to establish adaptations in a population." This definition conflates current utility with historical genesis. What is to be done with useful structures not built by natural selection for their current role?

III. A Definition of Exaptation

We have identified confusion surrounding one of the central concepts in evolutionary theory. This confusion arises, in part, because the taxonomy of form in relation to fitness lacks a term. Following Williams (see Table 1), we may designate as an *adaptation* any feature that promotes fitness and was built by selection for its current role (criterion of *historical genesis*). The operation of an adaptation is its *function*. (Bock uses the term function somewhat differently, but we believe we are following the biological vernacular here.) We may also follow Williams in labelling the operation of a useful character not built by selection for its current role as an *effect*. (We designate as an effect only the usage of such a character, not the character itself, see p. 5.) But what is the unselected, but useful character itself to be called? Indeed it has no recognized name (unless we accept Bock's broad definition of adaptation—the criterion of current utility alone—and reject both Darwin and Williams). Its space on the logical chart is currently blank.

We suggest that such characters, evolved for other usages (or for no function at all), and later "coopted" for their current role, be called *exaptations*. (See VIA on the related concept of "preadaptation.") They are fit for their current role, hence *aptus*, but they were not designed for it, and are therefore not *ad aptus*, or pushed towards fitness. They owe their fitness to features present for other reasons, and are therefore *fit* (*aptus*) *by reason of* (*ex*) their form, or *ex aptus*. Mammalian sutures are an exaptation for parturition. Adaptations have functions; exaptations have effects. The general, static phenomenon of being fit should be called aptation, not adaptation. (The set of aptations existing at any one time consists of two partially overlapping subsets: the subset of adaptations and the subset of exaptations. This also applies to the more inclusive set of aptations existing through time; see Table 1.)

IV. The Current Need for a Concept of Exaptation

Why has this conflation of historical genesis with current utility attracted so little attention heretofore? Every biologist surely recognizes that some useful characters did not arise by selection for their current roles; why have we not honored that knowledge with a name? Does our failure to do so simply underscore the unimportance of the subject? Or might this absent term, in Foucault's sense, reflect a conceptual structure that excluded it? And, finally, does the potential need for such a term at this time indicate that the conceptual structure itself may be altering?

Why did Williams not suggest a term, since he clearly recognized the problem and did separate usages into functions and effects (corresponding respectively to adaptations and to the unnamed features that we call exaptations)? Why did Bock fail to specify the problem at all? We suspect that the conceptual framework of modern evolutionary thought, by continually emphasizing the supreme importance and continuity of adaptation and natural selection at all levels, subtly relegated the issue of exaptation to a periphery of unimportance. How could nonadaptive aspects of form gain a proper hearing under Bock's definition (1967, p. 63): "On theoretical grounds, all existing features of animals are adaptive. If they were not adaptive, then they would be eliminated by selection and would disappear." Williams recognized the phenomenon of exaptation and even granted it some importance (in assessing the capacities of the human mind, for example), but he retained a preeminent role for adaptation and often designated effects as fortuitous or peripheral—"merely an incidental consequence" he states in one passage (p. 8).

We believe that the adaptationist program of modern evolutionary thought (Gould and Lewontin 1979) has been weakening as a result of challenges from all levels, molecules to macroevolution. At the biochemical level, we have theories of neutralism and suggestions that substantial amounts of DNA may be nonadaptive at the level of the phenotype (Orgel and Crick 1980; Doolittle and Sapienza 1980). Students of macroevolution have argued that adaptations in populations translate as effects to yield the patterns of differential species diversification that may result in evolutionary trends (Vrba's effect hypothesis, 1980). If nonadaptation (or what should be called nonaptation) is about to assume an important role in a revised evolutionary theory, then our terminology of form must recognize its cardinal evolutionary significance—cooptability for fitness (see Seilacher 1972, on important effects of a nonaptive pattern in the structure and coloration of molluscs).

Some colleagues have said that they prefer Bock's broad definition because it is more easily operational. We can observe and experiment to determine what good a feature does for an organism now. To reconstruct the historical pathway of its origin is always more difficult and often (when crucial evidence is missing) intractable.

To this we reply that we are not trying to dismantle Bock's concept. We merely argue that it should be called aptation (with adaptation and exaptation as its modes). As aptation, it retains all the favorable properties for testing enumerated above.

Historical genesis is, undoubtedly, a more difficult problem but we cannot therefore ignore it. As evolutionists, we are charged, almost by definition, to regard historical pathways as the essence of our subject. We cannot be indifferent to the fact that similar results can arise by different historical routes. Moreover, the distinction between ad- and exaptation, however difficult, is not unresolvable. If we ever find a small running dinosaur, ancestral to birds and clothed with feathers, we will know that early feathers were exaptations, not adaptations, for flight.

V. Examples of Exaptation

A) Feathers and flight-sequential exaptation in the evolution of birds.—Consider a common scenario from the evolution of birds. (We do not assert its correctness, but only wish to examine appropriate terminology for a common set of hypotheses.) Skeletal features, including the sternum, rib basket and shoulder joint, in late Jurassic fossils of *Archaeopteryx* indicate that this earliest known bird was probably capable of only the simplest feats of flight. Yet it was quite thoroughly feathered. This has suggested to many authors that selection for the initial development of feathers in an ancestor was for the function of insulation and not for flight (Ostrom 1974, 1979; Bakker 1975). Such a fundamental innovation would, of course, have many small as well as far-reaching, incidental consequences. For example, along no descendant lineage of this first feathered species did (so far as we know) a furry covering of the body evolve. The fixation early in the life of the embryo, of cellular changes that lead on the one hand to hair, and on the other to feathers, constrained the subsequent course of evolution in body covering (Oster 1980).

Archaeopteryx already had large contour-type feathers, arranged along its arms in a pattern very much as in the wings of modern birds. Ostrom (1979, p. 55) asks: "Is it possible that the initial (pre-*Archaeopteryx*) enlargement of feathers on those narrow hands might have been to increase the hand surface area, thereby making it more effective in catching insects?" He concludes (1979, p. 56): "I do believe that the predatory design of the wing skeleton in *Archaeopteryx* is strong evidence of a prior predatory function of the proto-wing in a cursorial proto-*Archaeopteryx*." Later selection for changes in skeletal features and feathers, and for specific neuromotor patterns, resulted in the evolution of flight.

The Black Heron (or Black Egret, *Egretta ardesiaca*) of Africa, like most modern birds, uses its wings in flight. But it also uses them in an interesting way to prey on small fish: "Its fishing is performed standing in shallow water with wings stretched out and forward, forming an umbrella-like canopy which casts a shadow on the water. In this way its food can be seen"

(McLachlan and Liversidge 1978, p. 39, Plate 6). This "mantling" of the wings appears to be a characteristic behavior pattern, with a genetic basis. The wing and feather structures themselves do not seem to be modified in comparison with those of closely related species, the individuals of which do not hunt in this way (A. C. Kemp, pers. comm.).

We see, in this scenario, a sequential set of adaptations, each converted to an exaptation of different effect that sets the basis for a subsequent adaptation. By this interplay, a major evolutionary transformation occurs that probably could not have arisen by purely increasing adaptation. Thus, the basic design of feathers is an adaptation for thermoregulation and, later, an exaptation for catching insects. The development of large contour feathers and their arrangement on the arm arise as adaptations for insect catching and become exaptations for flight. Mantling behavior uses wings that arose as an adaptation for flight. The neuromotor modifications governing mantling behavior, and therefore the mantling posture, are adaptations for fishing. The wing per se is an exaptation in its current effect of shading, just as the feathers covering it also arose in different adaptive contexts but have provided much evolutionary flexibility for other uses during the evolution of birds.

B) Bone as storage and support.—The development of bone was an event of major significance in the evolution of vertebrates. Without bone, vertebrates could not have later taken up life on land. Halstead (1969) has investigated the question: granting its subsequent importance as body support in the later evolution of vertebrates, why did bone evolve at such an early stage in vertebrate history? Some authors have hypothesized that bone initially arose as an osmoregulatory response to life in freshwater. Others, like Romer (1963), postulate initial adaptation of bony "armor" for a protective function. Pautard (1961, 1962) pointed out that any organism with much muscular activity needs a conveniently accessible store of phosphate. Following Pautard, and noting the seasonal cycle of phosphate availability in the sea, Halstead (1969) suggested the following scenario: Calcium phosphates, laid down in the skin of the earliest vertebrates, evolved initially as an adaptation for storing phosphates needed for metabolic activity. Only considerably later in evolution did bone replace the cartilaginous endoskeleton and adopt the function of support for which it is now most noted.

Thus, bone has two major uses in extant vertebrates: support/protection and storage/homeostasis (as a storehouse for certain mineral ions, including phosphate ions). The ions in vertebrate bone are in equilibrium with those in tissue fluids and blood, and function in certain metabolic activities (Scott and Symons 1977). For instance, in humans, 90% of body phosphorus is present in the inorganic phase of bone (Duthie and Ferguson 1973).

Following Halstead's analysis, the deposition of phosphate in body tissues originally evolved as an adaptation for a storage/metabolic function. The metabolic mechanism for producing bone per se can thus be interpreted as an exaptation for support. The metabolic mechanisms for depositing an increased quantity of phosphates and for mineralization, as well as the arrangement of bony elements in an internal skeleton, are then adaptations for support.

C) The evolution of mammalian lactation.—Dickerson and Geis (1969) recount how Alexander Fleming, in 1922, discovered the enzyme lysozyme. He had a cold and, for interest's sake, added a few drops of nasal mucus to a bacterial culture. To his surprise he found, after a few days, that something in the mucus was killing the bacteria: the enzyme lysozyme, since found in most bodily secretions and in large quantities in the whites of eggs. Lysozyme destroys many bacteria by lysing, or dissolving, the mucopolysaccharide structure of the cell wall. The amino acid sequence of α-lactalbumin, a milk protein of previously unknown function, was then found to be so close to that of lysozyme, that some relationship of close homology must be involved. Dickerson and Geis (1969, pp. 77–78) write:

> α-Lactalbumin by itself is not an enzyme but was found to be one component of a two-protein lactose synthetase system, present only in mammary glands during lactation . . . . The other component (the "A" protein) had been discovered in the liver and other organs as an enzyme for the synthesis of N-acetyllac-

> tosamine from galactose and NAG. But the combination of the A protein and α-lactalbumin synthesizes the milk sugar lactose from galactose and glucose instead. The non-catalytic α-lactalbumin evidently acts as a control device to switch its partner from one potential synthesis to another . . . . It appears that when a milk-producing-system was being developed during the evolution of mammals, and when a need for a polysaccharide-synthesizing enzyme arose, a suitable one was found in part by modifying a pre-existing polysaccaride-cutting enzyme.

Thus, lysozyme, in all vertebrates in which it occurs, is probably an adaptation for the function of killing bacteria. Further evolution in mammals (alteration of a duplicated gene according to Dickerson and Geis, 1969) resulted in α-lactalbumin, an adaptation (together with the A protein) for the function of lactose synthesis and lactation. Human lysozyme, in this scenario, is an adaptation for lysing the cell walls of bacteria, and an exaptation with respect to the lactose synthetase system.

D) Sexual "mimicry" in hyenas.—Females of the spotted hyena, *Crocuta crocuta,* are larger than males and dominant over them. Pliny, and other ancient writers, had already recognized a related and unusual feature of their biology in calling them hermaphrodites (falsely, as Aristotle showed). The external genitalia of females are virtually indistinguishable from the sexual organs of males by sight. The clitoris is enlarged and extended to form a cylindrical structure with a narrow slit at its distal end; it is no smaller than the male's penis and can also be erected. The *labia majora* are folded over and fused along the midline to form a false scrotal sac (though without testicles of course), virtually identical in form and position with the male's scrotum (Harrison Matthews 1939).

The literature on this sexual "mimicry" is full of speculations about adaptive meaning. Most of these arguments have conflated current utility and historical genesis in assuming that the demonstration of modern use (Bockian adaptation) specifies the path of origin (adaptation as used by Williams and Darwin, and as advocated in this paper). We suggest that the absence of an articulated concept of exaptation has unconsciously forced previous authors into this erroneous conceptual bind.

Kruuk (1972), the leading student of spotted hyenas, for example, notes that the enlarged sexual organs of females are used in an important behavior know as the meeting ceremony. Hyenas spend long periods as solitary wanderers searching for carrion, but they also live in well integrated clans that defend territory and engage in communal hunting. A mechanism for reintegrating solitary wanderers into their proper clan must be developed. In the meeting ceremony, two hyenas stand side to side, facing in opposite directions. Each lifts the inside hind leg, exposing an erect penis or clitoris to its partner's teeth. They sniff and lick each other's genitals for 10 to 15 seconds, largely at the base of the penis or clitoris and in front of the scrotum or false scrotum.

Having discovered a current utility for the prominent external genitalia of females, Kruuk (1972, pp. 229–230) infers that they must have evolved for this purpose:

> It is impossible to think of any other purpose for this special female feature than for use in the meeting ceremony . . . . It may also be, then, that an individual with a familiar but relatively complex and conspicuous structure sniffed at during the meeting has an advantage over others; the structure would often facilitate this reestablishment of social bonds by keeping partners together over a longer meeting period. This could be the selective advantage that has caused the evolution of the females' and cubs' genital structure.

Yet another hypothesis, based upon facts known to every Biology I student, virtually cries out for recognition. The penis and clitoris are homologous organs, as are the scrotum and labia majora. We know that high levels of androgen induce the enlargement of the clitoris and the folding over and fusion of the labia until they resemble penis and scrotal sac respectively. (In fact, in an important sense, they *are* then a penis and scrotal sac, given the homologies.) Human baby girls with unusually enlarged adrenals secrete high levels of androgen, and are born with a peniform clitoris and an empty scrotal sac formed of the fused labia.

Female hyenas are larger than males and

dominant over them. Since these features are often hormonally mediated in mammals, should we not conjecture that females attain their status by secreting androgens and that the peniform clitoris and false scrotal sac are automatic, secondary by-products. Since they are formed anyway, a later and secondary utility might ensue; they may be coopted to enhance fitness in the meeting ceremony and then secondarily modified for this new role. We suggest that the peniform clitoris and false scrotal sac arose as nonaptive consequences of high androgen levels (a primary adaptation related to the unusual behavioral role of females). They are, therefore, exaptations for the meeting ceremony, and their effect in enhancing fitness through that ceremony does not specify the historical pathway of their origin.

Yet this obvious hypothesis, with its easily testable cardinal premise, was not explicitly examined until 1979 after, literally, more than 2000 years of speculation in the adaptive mode (both ancient authors and medieval bestiaries tried to infer God's intent in creating such an odd beast). Racey and Skinner (1979) found no differences in levels of androgen in blood plasma of male and female spotted hyenas. Female fetuses contained the same high level of testosterone as adult females. In the other two species of the family Hyaenidae, however, androgen levels in blood plasma are much lower for females than for males. Females of these species are not dominant over males and do not develop peniform clitorises or false scrotal sacs.

We do not assert that our alternative hypothesis of exaptation must be correct. One could run the scenario in reverse (with a bit of forcing in our judgment): females "need" prominent genitalia for the meeting ceremony; they build them by selection for high androgen levels; large size and dominance are a secondary by-product of the androgen. We raise, rather a different issue: why was this evident alternative not considered, especially by Kruuk in his excellent exhaustive book on the species? We suggest that the absence of an explicitly articulated concept of exaptation has constrained the range of our hypotheses in subtle and unexamined ways.

E) The uses of repetitive DNA.—For a few years after Watson and Crick elucidated the structure of DNA, many evolutionists hoped that the architecture of genetic material might fit all their presuppositions about evolutionary processes. The linear order of nucleotides might be the beads on a string of classical genetics: one gene, one enzyme; one nucleotide substitution, one minute alteration for natural selection to scrutinize. We are now, not even 20 years later, faced with genes in pieces, complex hierarchies of regulation and, above all, vast amounts of repetitive DNA. Highly repetitive, or satellite, DNA can exist in millions of copies; middle-repetitive DNA, with its tens to hundreds of copies, forms about one quarter of the genome in both *Drosophila* and *Homo*. What is all the repetitive DNA for (if anything)? How did it get there?

A survey of previous literature (Doolittle and Sapienza 1980; Gould 1981) reveals two emerging traditions of argument, both based on the selectionist assumption that repetitive DNA must be good for something if so much of it exists. One tradition (see Britten and Davidson 1971 for its *locus classicus*) holds that repeated copies are conventional adaptations, selected for an immediate role in regulation (by bringing previously isolated parts of the genome into new and favorable combinations, for example, when repeated copies disperse among several chromosomes). We do not doubt that conventional adaptation explains the preservation of much repeated DNA in this manner.

But many molecular evolutionists now strongly suspect that direct adaptation cannot explain the existence of all repetitive DNA: there is simply too much of it. The second tradition therefore holds that repetitive DNA must exist because evolution needs it so badly for a flexible future—as in the favored argument that "unemployed," redundant copies are free to alter because their necessary product is still being generated by the original copy (see Cohen 1976; Lewin 1975; and Kleckner 1977, all of whom also follow the first tradition and argue both sides). While we do not doubt that such future uses are vitally important consequences of repeated DNA, they simply cannot be the cause of its existence, unless we return to certain theistic views that permit the control of present events by future needs.

This second tradition expresses a correct intuition in a patently nonsensical (in its nonpejorative meaning) manner. The missing thought that supplies sense is a well articulated concept of exaptation. Defenders of the second tradition understand how important repetitive DNA is to evolution, but only know the conventional language of adaptation for expressing this conviction. But since utility is a future condition (when the redundant copy assumes a different function or undergoes secondary adaptation for a new role), an impasse in expression develops. To break this impasse, we might suggest that repeated copies are nonapted features, available for cooptation later, but not serving any direct function at the moment. When coopted, they will be exaptations in their new role (with secondary adaptive modifications if altered).

What then is the source of these exaptations? According to the first tradition, they arise as true adaptations and later assume their different function. The second tradition, we have argued, must be abandoned. A third possibility has recently been proposed (or, rather, better codified after previous hints): perhaps repeated copies can originate for no adaptive reason that concerns the traditional Darwinian level of phenotypic advantage (Orgel and Crick 1980; Doolittle and Sapienza 1980). Some DNA elements are transposable; if these can duplicate and move, what is to stop their accumulation as long as they remain invisible to the phenotype (if they become so numerous that they begin to exert an energetic constraint upon the phenotype, then natural selection will eliminate them)? Such "selfish DNA" may be playing its own Darwinian game at a genic level, but it represents a true nonaptation at the level of the phenotype. Thus, repeated DNA may often arise as a nonaptation. Such a statement in no way argues against its vital importance for evolutionary futures. When used to great advantage in that future, these repeated copies are exaptations.

VI. Significance of Exaptation

A) A solution to the problem of preadaptation.—The concept of preadaptation has always been troubling to evolutionists. We acknowledge its necessity as the only Darwinian solution to Mivart's (1871) old taunt that "incipient stages of useful structures" could not function as the perfected forms do (what good is 5% of a wing). The incipient stages, we argue, must have performed in a different way (thermoregulation for feathers, for example). Yet we traditionally apologize for "preadaptation" in our textbooks, and laboriously point out to students that we do not mean to imply foreordination, and that the word is somehow wrong (though the concept is secure). Frazzetta (1975, p. 212), for example, writes: "The association between the word 'preadaptation' and dubious teleology still lingers, and I can often produce a wave of nausea in some evolutionary biologists when I use the word unless I am quick to say what I mean by it."

Indeed, the word is wrong and our longstanding intuitive discomfort is justified (see Lambert, MS). For if we divide the class of features contributing to fitness into adaptations and exaptations, and if adaptations were constructed (and exaptations coopted) for their current use, then features working in one way cannot be pre*ad*aptations to a different and subsequent usage: the term makes no sense at all.

The recognition of exaptation solves the dilemma neatly, for what we now incorrectly call "preadaptation" is merely a category of exaptation considered before the fact. If feathers evolved for thermoregulation, they become exaptations for flight once birds take off. If, however, with the hindsight of history, we choose to look at feathers while they still encase the running, dinosaurian ancestors of birds, then they are only potential exaptations for flight, or *preaptations* (that is, *aptus*—or fit—before their actual cooptation). The term "preadaptation" should be dropped in favor of "preaptation." Preaptations are potential, but unrealized, exaptations; they resolve Mivart's major challenge to Darwin.

B) Primary exaptations and secondary adaptations.—Feathers, in their basic design, are exaptations for flight, but once this new effect was added to the function of thermoregulation as an important source of fitness, feathers underwent a suite of secondary adaptations (sometimes called post-adaptations) to enhance their utility in flight. The order and arrangement of tetrapod limb bones is an exaptation for walking on land; many modifications of shape and musculature are secondary adaptations for terrestrial life.

The evolutionary history of any complex feature will probably include a sequential mixture of adaptations, primary exaptations and secondary adaptations. Just as any feature is plesiomorphic at one taxonomic level and apomorphic at another (torsion in the class Gastropoda and in the phylum Mollusca), we are not disturbed that complex features are a mixture of exaptations and adaptations. Any coopted structure (an exaptation) will probably not arise perfected for its new effect. It will therefore develop secondary adaptations for the new role. The primary exaptations and secondary adaptations can, in principle, be distinguished.

C) The sources of exaptation.—Features coopted as exaptations have two possible previous statuses. They may have been adaptations for another function, or they may have been non-aptive structures. The first has long been recognized as important, the second underplayed. Yet the enormous pool of nonaptations must be the wellspring and reservoir of most evolutionary flexibility. We need to recognize the central role of "cooptability for fitness" as the primary evolutionary significance of ubiquitous nonaptation in organisms. In this sense, and at its level of the phenotype, this nonaptive pool is an analog of mutation—a source of raw material for further selection.

Both adaptations and nonaptations, while they may have non-random proximate causes, can be regarded as randomly produced with respect to any potential cooptation by further regimes of selection. Simply put: all exaptations *originate* randomly with respect to their effects. Together, these two classes of characters, adaptations and nonaptations, provide an enormous pool of variability, at a level higher than mutations, for cooptation as exaptations. (Lambert, MS, has discussed this with respect to preadaptations only—preaptations in our terminology. He explored the evolutionary implications of the notion that for any function, resulting directly from natural selection at any one time, there may be multiple effects.)

If all exaptations began as adaptations for another function in ancestors, we would not have written this paper. For the concept would be covered by the principle of "preadaptation"—and we would only need to point out that "preaptation" would be a better term, and that etymology requires a different name for preaptations after they are established. Exaptations that began as nonaptations represent the missing concept. They are not covered by the principle of preaptation, for they were not adaptations in ancestors. They truly have no name, and concepts without names cannot be properly incorporated in thought. The great confusions of historical genesis and current utility primarily involve useful features that were not adaptations in ancestors—as in our examples of sexual "mimicry" in hyenas and the uses of middle-repetitive DNA.

D) The irony of our terminology for nonaptation.—It seems odd to define an important thing by what it is not. Students of early geology are rightly offended that we refer to $^5/_6$ of earth history as Precambrian. Features not now contributing to fitness are usually called nonadaptations. (In our terminology they are nonaptations.) This curious negative definition can only record a feeling that the subject is "lesser" than the thing it is not. We believe that this feeling is wrong, and that the size of the pool of nonaptations is a central phenomenon in evolution. The term "nonadaptive" is but another indication of previous—and in our view false—convictions about the supremacy of adaptation. The burden of nomenclature is already great enough in this paper and we do not propose a new term for features without current fitness. But we do wish to record the irony.

E) Process and state-of-being.—Evolutionary biologists use the term adaptation to describe both a current state-of-being (as discussed in this paper) and the process leading to it. This duality presents no problem in cases of true adaptation, where a process of selection directly produces the state of fitness. Exaptations, on the other hand, are not fashioned for their current role and reflect no attendant process beyond cooptation (Table 1); they were built in the past either as nonaptive by-products or as adaptations for different roles.

Perhaps we should begin our analysis of process with a descriptive approach and simply focus upon the set of features that increase their relative or absolute abundance within populations, species or clades by the only general processes that can yield such "plurifaction," or "more making": differential branching or persistence (see Arnold and Fristrup, MS). This descriptive process of plurifaction has two basic causes. First, features may increase their representation actively by contributing to branching or persistence either as adaptations evolved by selection for their current function, or exaptations evolved by another route and coopted for their useful effect. Secondly, and particularly at the higher level of species within clades, features may increase their own representation for a host of nonaptive reasons, including causal correlation with features contributing to fitness, and fortuitous correlation found at such surprisingly high frequency in random simulations by Raup and Gould (1974). These nonaptive features establish an enormous pool for potential exaptation.

VII. Conclusion

The ultimate decision about whether we have written a trivial essay on terminology or made a potentially interesting statement about evolution must hinge upon the importance of exaptation, both in frequency and in role. We believe that the failure of evolutionists to codify such a concept must record an inarticulated belief in its relative insignificance.

We suspect, however, that the subjects of nonaptation and cooptability are of paramount importance in evolution. (When cooptability has been recognized—in the principle of "preadaptation"—we have focussed upon shift in role for features previously adapted for something else, not on the potential for exaptation in nonapted structures.) The flexibility of evolution lies in the range of raw material presented to processes of selection. We all recognize this in discussing the conventional sources of genetic variation—mutation, recombination, and so forth—presented to natural selection from the genetic level below. But we have not adequately appreciated that features of the phenotype themselves (with their usually complex genetic bases) can also act as variants to enhance and restrict future evolutionary change. Thus the important statement of Fisher's fundamental theorem considers only genetic variance in relation to fitness: "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time" (Fisher 1958). In an analogous way, we might consider the flexibility of phenotypic characters as a primary enhancer of or damper upon future evolutionary change. Flexibility lies in the pool of features available for cooptation (either as adaptations to something else that has ceased to be important in new selective regimes, as adaptations whose original function continues but which may be coopted for an additional role, or as nonaptations always potentially available). The paths of evolution—both the constraints and the opportunities—must be largely set by the size and nature of this pool of potential exaptations. Exaptive possibilities define the "internal" contribution that organisms make to their own evolutionary future.

A. R. Wallace, a strict adaptationist if ever there was one, nonetheless denied that natural selection had built the human brain. "Savages" (living primitives), he argued, have mental equipment equal to ours, but maintain only a rude and primitive culture—that is, they do not use most of their mental capacities and natural selection can only build for immediate use. Darwin, who was not a strict adaptationist, was both bemused and angered. He recognized the hidden fallacy in Wallace's argument: that the brain, though undoubtedly built by selection for some complex set of functions, can, as a result of its intricate structure, work in an unlimited number of ways quite unrelated to the selective pressure that constructed it. Many of these ways might become important, if not indispensable, for future survival in later social contexts (like afternoon tea for Wallace's contemporaries). But current utility carries no automatic implication about historical origin. Most of what the brain now does to enhance our survival lies in the domain of exaptation—and does not allow us to make hypotheses about the selective paths of human history. How much of the evolutionary literature on human behavior would collapse if we incorporated the principle of exaptation into the core of our evolutionary thinking? This collapse would be constructive because it would vastly broaden our range of hypotheses, and focus attention on current function and development (all testable propositions) instead of leading us to unprovable reveries about primal fratricide on the African savanna or dispatching mammoths at the edge of great ice sheets—a valid subject, but one better treated in novels that can be quite enlightening scientifically (Kurtén 1980).

Consider also the apparently crucial role that repeated DNA has played in the evolution of phenotypic complexity in organisms. If each gene codes for an indispensable enzyme (or performs any necessary function), asks Ohno (1970) in his seminal book, how does evolution transcend mere tinkering along established lines and achieve the flexibility to build new types of organization. Ohno argues that this flexibility must arise as the incidental result of gene duplication, with its production of redundant genetic material: "Had evolution been entirely dependent upon natural selection, from a bacterium only numerous forms of bacteria would have emerged. . . . Only the cistron which became redundant was able to escape from the relentless pressure of natural selection, and by escaping, it accumulated formerly forbidden mutations to emerge as a new gene locus" (from the preface to Ohno 1970).

We argued in section VE that much of this repetitive DNA may arise for nonaptive reasons at the level of the individual phenotype (as in the "selfish DNA" hypothesis). The repeated copies are then exaptations, coopted for fitness and secondarily adapted for new roles. And they are exaptations in the interesting category of structures that arose as nonaptations, when the "selfish DNA" hypothesis applies.

Thus, the two evolutionary phenomena that may have been most crucial to the development of complexity with consciousness on our planet (if readers will pardon some dripping anthropocentrism for the moment)—the process of creating genetic redundancy in the first place, and the myriad and inescapable consequences of building any computing device as complex as the human brain—may both represent exaptations that began as nonaptations, the concept previously missing in our evolutionary terminology. With examples such as these, the subject cannot be deemed unimportant!

In short, the codification of exaptation not only identifies a common flaw in much evolutionary reasoning—the inference of historical genesis from current utility. It also focusses attention upon the neglected but paramount role of nonaptive features in both constraining and facilitating the path of evolution. The argument is not anti-selectionist, and we view this paper as a contribution to Darwinism, not as a skirmish in a nihilistic vendetta. The main theme is, after all, cooptability for *fitness*. Exaptations are vital components of any organism's success.

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