

**Thank you for using the
University at Albany's
UA Delivery Service**

NOTICE WARNING CONCERNING COPYRIGHT RESTRICTIONS

The copyright law of the United States (Title 17, United States Code) governs the making of photocopies or other reproductions of copyrighted material. Under certain conditions specified in the law, libraries and archives are authorized to furnish a photocopy or other reproduction. One of these specific conditions is that the photocopy or reproduction is not to be "used for any purpose other than private study, scholarship, or research." If a user makes a request for, or later uses, a photocopy or reproduction for purposes in excess of "fair use," that user may be liable for copyright infringement. This institution reserves the right to refuse a copying order if, in its judgment, fulfillment of the order would involve violation of copyright law.

Exaptation: A Crucial Tool for an Evolutionary Psychology

Stephen Jay Gould

Harvard University

Evolutionary theory lacks a term for a crucial concept—a feature, now useful to an organism, that did not arise as an adaptation for its present role, but was subsequently coopted for its current function. I call such features “exaptations” and show that they are neither rare nor arcane, but dominant features of evolution—though previously unappreciated in the context of the overly adaptationist neo-Darwinian theory. This article argues that exaptation overcomes the fallacy of human sociobiology, helps us to understand the major patterns of flexibility and contingency in life’s history, revises the roles of structure and function in evolutionary theory, serves as a centerpiece for grasping the origin and meaning of brain size in human evolution, and thereby cries out for recognition as a key to evolutionary psychology. Historical origin and current utility are distinct concepts and must never be conflated.

A Terminological Odyssey

In his classic treatise, “On the Nature of Limbs,” published in 1849, Richard Owen presented a conundrum for biologists committed to the principle of adaptation—a word and concept of ancient pedigree, long antedating Darwin’s later explanation in terms of evolution by natural selection. Mammals, and humans especially, must begin life with a tight squeeze—the passage of the relatively large fetal head through the narrow birth canal. The bones of the skull are not yet fully ossified or sutured together. Consequently, the nonrigid head can be “molded” as the bones alter their positions to allow this first essential adjust-

Correspondence regarding this article should be addressed to Stephen Jay Gould, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

ment to extrauterine life. If this molding could not occur, birth with such a large head would be impossible. Thus, we seem to have a *prima facie* case for a *vitaly important adaptation* in this delayed ossification of skull bones. After all, big heads are a key to human success, and delayed ossification permits big heads. (With limited brain growth after birth, small neonatal heads and later expansion may not represent an option for an alternative pathway.)

Yet Owen, Britain's greatest vertebrate anatomist and first director of the independent natural history branch of the British Museum, denied that delayed ossification could rank as a mammalian adaptation—for the excellent reason that “lower” vertebrates (and mammalian ancestors), which need only to break free from an egg, share this feature with us. Owen wrote, linking the case to a general critique of adaptationism by way of Sir Francis Bacon's famous simile about the barrenness of teleology in general:

Such a final purpose is indeed readily perceived and admitted in regard to the multiplied points of ossification of the skull of the human fetus, and their relation to safe parturition. But when we find that the same ossific centers are established, and in similar order, in the skull of the embryo kangaroo, which is born when an inch in length, and in that of the callow bird that breaks the brittle egg, we feel the truth of Bacon's comparison of “final causes” to the Vestal Virgins, and perceive that they would be barren and unproductive of the fruits we are laboring to attain. (1849, p. 40)

Charles Darwin, whose strongly adaptationist theory set the problem (by imposing limits to thought) that this paper addresses, took Owen's point and example to heart, and repeated the case in a cautionary note on overindulgence in adaptationist explanation (Darwin, 1859, p. 197):

The sutures in the skull 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.

This case raises some of the deepest issues in evolutionary theory but, for now, let me pose a question almost laughably trivial in comparison (yet deceptively profound as an opening to the generalities): If the term “adaptation” be inappropriate for reasons given by Owen and Darwin, what shall we call this eminently useful delay of ossification in the human embryo? We cannot maintain a clear concept if we have no name for the primary phenomenon so illustrated.

We might honor the fact that delayed ossification did not arise “for” its current role in parturition by calling it a “nonadaptation” or a “nonaptation” (and such cumbersome terms are in frequent use, by yours truly among others—see Gould, 1984). But such a resolution would be unsatisfactory for at least two reasons beyond infelicity: (a) active concepts should not be defined negatively by what they are not, and (b) “nonaptation” would not get at the heart of the

evolutionary meaning of the phenomenon—that a useful structure may arise for other reasons and then be coopted for its present role.

I can imagine two solutions to this terminological problem:

1. We might extend “adaptation”—the great warhorse term of Darwinian evolution—to cover this phenomenon. Delayed ossification is useful in parturition, and “adaptation” is about use—so why not extend a term for a *process of building utility* into a general description for the *state of utility*, whatever its origin? (Insofar as evolutionary biologists have considered the issue at all, they have favored this extension. Nonetheless, most extensions of “adaptation” from process to state do not represent an active decision, consciously devised and defended, but rather a passive oozing forth of a favored term beyond a logical border into a defenseless territory. Many biologists have not even considered the crucial difference between historical origin and current utility. In a thoughtless analog of the contemporary motto “if it feels good, do it,” they have simply taken the line, “if it works, call it adaptation.”) But this extension should be rejected for two reasons:

(a) *Historical*. Adaptation, throughout the history of English usage in biology, has been a “process term,” not a “state term.” This definition inheres in etymology, for an adaptation is, literally, something fit (*aptus*) by active construction for (*ad*) its usage. The process meaning conforms with vernacular use; we can adapt a bicycle for a young beginner by installing training wheels, but no one would call a credit card an adaptation for opening certain kinds of locked doors, even though the card works as well for this purpose as does the altered bike for a stable ride. Moreover, and most importantly, the process definition affirms a long tradition of professional usage within evolutionary biology. The previous quotation from Darwin himself clearly supports the “process” definition—for Darwin states that some colleagues have called delayed ossification an adaptation, but they are wrong because this eminently useful feature has been coopted, rather than built for, successful parturition. This usage enjoys an unbroken pedigree, and is explicitly defended in the most important modern work on adaptation—for Williams (1966, p. 6) argues that we should speak of adaptation only if we can “attribute the origin and perfection of this design to a long period of selection for effectiveness in this particular role.”

(b) *Conceptual and utilitarian*. For a historical scientist, no conceptual tool can be more important than the clear separation of *historical origin* and *current utility*. The false conceptual passage from present function to initial construction ranks with the post hoc fallacy and the confusion of correlation with cause as primary errors of reasoning about temporal sequences. We all understand this principle in the case of human artifacts: No one would claim that the U.S. Mint made dimes thin so that all Americans could carry surrogate screwdrivers in their change purses. And we all laugh at Voltaire's Dr. Pangloss when

he exclaims: "Everything is made for the best purpose. Our noses were made to carry spectacles, so we have spectacles. Legs were clearly intended for breeches, and we wear them."

2. We might recognize a lacuna (favorite fancy word of scholars, though the vernacular "gap" will do nicely) in current terminology and coin a new term for the important phenomenon illustrated by the case of delayed ossification—i.e., vital current utility based on cooptation of structures evolved in other contexts and for other purposes (or perhaps for no purpose at all). We who dwell in the jargon-polluted groves of academe should propose new words only with the greatest caution, in the direst of circumstances, and in the absence of any other reasonable solution to a problem. The most compelling justification for a new term resides in conceptual gaps and persistent errors in thought reasonably connected with the absence of a category in the taxonomy of ideas. For a concept without a name often lies hidden from identification and use.

Elisabeth Vrba and I struggled with this issue in our attempts to formulate theories of large-scale evolutionary change. We finally decided that the absence of a term for "useful structures not evolved for their current function, but coopted from other contexts" had produced a sufficiently long-standing and serious muddle to warrant a new term by the criteria suggested above. We therefore proposed the term "exaptation" for "features that now enhance fitness, but were not built by natural selection for their current role" (Gould & Vrba, 1982, p. 4). The extent of immediate commentary (Lewin, 1982) and later usage and debate (Endler & McLellan, 1988; Gans, 1988; Pierce, 1988; Chatterton & Speyer, 1989; and many others) convinces us that, at the very least, we identified a conceptual weakness not sufficiently appreciated by evolutionary biologists in the past.

In our "taxonomy of fitness" (see Table 1), process, state (character), and

Table 1. A Taxonomy of Fitness

Process	Character	Usage
Natural selection shapes the character for a current use—adaptation	Adaptation	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 nonadaptation) is coopted for a current use—cooptation		

Source: Gould and Vrba (1982). Reprinted by permission.

usage must be distinguished. In the realm of process, traditional adaptation (Darwin's usage) occurs when natural selection shapes a feature for its current use. If characters are built for other reasons, and then "seized" for an altered utility, we speak (using a vernacular term) of "cooptation." Coopted characters may have been built by natural selection for a different function (e.g., the proto-wing, initially evolved as an adaptation for thermoregulation and later coopted for flight, according to the standard, classic conjecture), or may have arisen for no adaptive purpose at all (e.g., as a sequel or consequence of another adaptation, in what Darwin called "correlation of growth"). In either case, coopted structures will probably undergo some secondary modification—counting as superimposed, true adaptation—for the newly seized function. (The feather, for example, will need some redesign for efficient flight—as we can scarcely imagine that a structure evolved for thermoregulation would be accidentally and optimally suited for something so different as aerial locomotion.) But such secondary tinkering does not alter the primary status of such a structure as coopted rather than adapted.

For current state, we reluctantly permit *stare decisis* in retaining "adaptation" for characters built by selection for their current use. (We assume, for example, that the elaborate plumages and behavioral displays of male birds of paradise are true adaptation for mating success.) We do regret the retention of the same word—adaptation—for both a process and a utility arising by the process, but we bow to entrenched convention here. We then fill the previous gap by coining *exaptation* for useful structures coopted from other contexts—for such structures are fit (*aptus*) not by explicit molding for (*ad*) current use, but as a consequence of (*ex*) properties built for other reasons.

We recognize, of course, that distinction of adaptation from exaptation requires knowledge of historical sequences—and that such evidence is often, probably usually, unavailable. In such cases, we may only know that a structure is currently useful—and we may be unable to identify the source of utility. In such cases, we urge that the neutral term "aptation" (encompassing both *ad*- and *ex*-aptation) be used in place of the conventional and falsely inclusive "adaptation." (Vrba and I are delighted that since publication of our revised taxonomy in 1982, this recommendation has been followed by many biologists—see Vermeij, 1987, and Allmon, in press—whatever their feeling about our term "exaptation.")

In the final category of usage, adaptations have functions, but "function" cannot describe the utility of an exaptation. To cite Williams' (1966) amusing but profound example, flying fishes fall back into the water by virtue of gravity, and this descent is essential to their continued existence. But weight, as an inevitable property of matter in Newton's world, is an exaptation for falling back, clearly not an adaptation. In ordinary English usage, we would not call falling back a function of weight. We therefore, following Williams, designate the utility of an

exaptation as an "effect" (again choosing vernacular English—falling back is an effect of weight).

One final point on terminology: Evolutionists have always recognized that some currently useful structures must be coopted rather than adapted—if only because cooptation provides the classical solution to the famous "problem of the incipient stages of useful structures." In plain English and concrete form, how can wings evolve for flight if 5% of a wing confers no conceivable aerodynamic benefit? The classical solution argues that wings evolved for something else (thermoregulation, in the most common scenario) and were then coopted.

In standard terminology, the proto-wing is called a "preadaptation" for flight. I doubt that any other evolutionary term has been so widely viewed as misleading and problematical. All teachers introduce "preadaptation" with an apology, disavowing the explicit etymological claim for foreordination, and explaining that the term really does not mean what it plainly says. But we did not decide to coin "exaptation" as a mere etymological nicety. If "preadaptation" had included all that "exaptation" now supplies, we would not have suggested our revision. As its major inadequacy, "preadaptation" covers only one of the two styles of cooptation, and therefore cannot subsume all exaptations. Preadaptations are built for one purpose, and then coopted for another (e.g., wings built for thermoregulation are coopted for flight). But what about the second category? — structures not built as adaptations at all, but later coopted for utilities just as vital (e.g., weight existing by virtue of the physics of matter, is then coopted for falling back into the water). Preadaptation does not cover the large domain of nonadaptations later coopted for utility — and "exaptation" is therefore needed to fill a substantial lacuna. I argue in the next section that the concept of coopted nonadaptation is the key to a proper evolutionary psychology for the human brain — and exaptation is therefore especially vital in human affairs.

I need hardly mention—for it forms the underlying theme of this paper—that the conceptual incubus of this entire tale is the overreliance on adaptation so characteristic of English evolutionary thought, and the insufficiently critical acceptance of this bias in cognate fields that, however properly, have borrowed evolutionary concepts for their own explanations.

The Cardinal Dilemma of an Evolutionary Psychology

As bodies, humans are a poor (or at best an average) work among mammals. Our insecure status between ape and angel arises from the state of our brains as "continuous with yet somehow transcending" (or at least awfully special—and I do mean "awful" in the old sense of inspiring awe). The truth of continuationism leads us to apply evolutionary concepts as keys to elucidating our own mental functioning—for should not the cardinal theory of biology

unlock the secrets of a structure that attained its unique power by evolving large size and attendant complexity? But the appearance of transcendence inspires us to seek something special to resolve something unique.

My own reaction to this dilemma (old-fashioned rationalist and materialist that I am) leads me toward the continuationist pole for two basic reasons. First, new qualities can arise from accretion and diversification of quantity—and human mental uniqueness might therefore emerge from a brain altered and enlarged under natural selection. Second, I recognize that affirmations of unbridgeable uniqueness represent the lingering solace of Western philosophical traditions more than any empirical claim upon our attention. But as I veer toward continuationism and evolutionary reductionism, I am stopped by the equally biased ills of that pole—particularly by the rationales for dubious social behaviors (from the colonial expansionism and industrial exploitation of Darwin's day, to modern sexism) that have been sought in evolutionary arguments. And if the 19th-century themes found their rationalization primarily in the evolutionary doctrine of progress (and the attendant notion of higher and lower people, based on race, class, or sex), the 20th-century version relies on adaptationism ("never say higher or lower," to quote Darwin, but empirical differences may be evolved solutions to disparate circumstances based on the preeminent calculus of individual reproductive success). And so—choose your metaphor—we are stuck between the horns of a dilemma, Scylla and Charybdis, a rock and a hard place. We want an evolutionary psychology, but the traditional offerings of evolutionists seem so wrongheaded. Do we abandon the quest, or do we seek a more adequate evolutionary version? This paper is dedicated to the latter solution—an attempt to steer between the horns.

The Horn of Scylla (Who Is Indeed a Rock)

We sense a basic fallacy (or at least an unconscious ideological embeddedness) in a proposed evolutionary psychology, but we are told that its proposals are deduced and necessary consequences of something worth our ultimate respect, and usually called "Darwinism," or simply "evolutionary theory"—so we must either take it, or leave the whole (and abstractly sensible) enterprise.

The latest widely bruited proposal for such an evolutionary psychology has been issued by the self-proclaimed discipline of sociobiology. (If "sociobiology" is used generically and loosely to refer to any evolutionary account of organismal behavior, then its status is unexceptionable and deniable only by creationists. Do any of us wish to assert that behavior does not evolve? The "sociobiology debate" has occurred because this term did not arise (and has not been used) generically, but quite specifically to label the particular style of theorizing advocated by E. O. Wilson (1975).

Wilson is a strict Darwinian (an ultra-Darwinist in the terminology of

Blanc, 1990). I have great respect for this powerful and coherent intellectual position, though I regard it as deeply wrong in the most interesting way (Gould, 1982; Gould & Lewontin, 1979; Vrba & Gould, 1986). Strict Darwinism is a monistic, one-level theory of evolutionary causation. It holds that, with exceptions of trivial relative frequency, all evolution occurs by natural selection acting upon individual organisms that are struggling (metaphorically to be sure) for personal reproductive success. Since such success must be measured in transmission of genes to the next generation, any behavior that maximizes the passage will be favored. In particular, an organism need not prevail by its own copulations; helping relatives who share enough genes may do just as well—hence Haldane's famous dictum as an evolutionary calculus: "I am prepared to lay down my life for more than 2 brothers or more than 8 first cousins" (reported in Hamilton, 1964/1971, p. 42). For this reason, kin selection, the central concept of modern sociobiology, is a buttress to ultra-Darwinism (not a statement about group selection—i.e., aid to unrelated others at a cost to oneself—as it is sometimes misinterpreted in popular accounts); for it takes behaviors (like altruism) that seem contrary to the key Darwinian belief in personal struggle and renders them adaptive in the service of individual reproductive success.

In my view, this Darwinian apparatus is true and powerful at its own level, but limited in scope both in its own domain (because constraints of many kinds, both positive and negative, have as much influence as natural selection in determining evolutionary pathways—see Gould, 1989) and in its power to explain evolution at infra- and supra-organismal levels (for selection and other evolutionary processes also occur at levels below and above individuals—on genes and species, for example—and a hierarchical account of causation is therefore required).

Adaptation is the key concept of ultra-Darwinism—for natural selection on individuals, in this view, holds almost exclusive sway, and natural selection produces adaptation (defined as genetically based forms and behaviors that foster individual reproductive success). Selection is difficult to ascertain directly, but its product—adaptation—is always present and palpable. Thus, the actual research program of ultra-Darwinism relies upon the identification of adaptations and the inference to their genetic basis and production by natural selection.

We now come to the crux of the fatal flaw in human sociobiology. As an ultra-Darwinian account of human behavior, the theory is committed to explanation in terms of adaptation. It must use the following general research strategy: break up the behavioral repertoire into items, posit an advantage for each item in terms of individual reproductive success, assume a genetic basis for the behavior (not necessarily direct), and then infer that natural selection built the item for its implied advantages in the great calculus of reproductive struggle.

The political debate on sociobiology has focused on the politically conservative implications of arguing that group differences in behavior (particularly

between the sexes) are naturally sanctioned as adaptations, and hard or impossible to alter as a consequence of their genetic basis. But it would be wrong to argue, as some have, that a political agenda motivated the theory. Rather, these consequences flow from ultra-Darwinian commitment to the hegemony of adaptation; they are logical entailments of a biological theory, not overt political programs masquerading as science.

Human sociobiology is fundamentally wrong because (for reasons elaborated in the next section) ultra-Darwinism, especially in its commitment to adaptationism, is fallacious (or at least vastly overextended)—not because many of us do not like its political implications. If any overt politics motivated the origin of human sociobiology, blame the academic jockeying of disciplinary extension, prestige, and imperialism (e.g., reduction of the social sciences to biology), not the larger social constructs of conservatism and laissez-faire. (And if you, as social scientists, wish to take a compassionate view of our efforts in biological imperialism—in a sermon-on-the-mount manner of loving one's adversaries—then do understand that we have often been subject to the same denigration by physicists and chemists. It is a sad fact that the oppressed often take up the tools of oppression.)

The Horn of Charybdis (Who, as a Whirlpool, Is Indeed a Hard Place)

Wilson did argue, and even illustrate pictorially (1975, p. 5), that the behavioral sciences as now constituted would be cannibalized to nothingness by absorption into cellular biology (on the one side) and into evolutionary biology (on the other). In the context of such a battlecry, I can hardly blame social scientists for rallying about their own flag, and digging deeper into their own trenches for defense of territorial integrity. And thus we understand the temptations of Charybdis; for if Scylla be the acceptance of thralldom, then Charybdis is the whirlpool of self-reference and exclusion of all external influence. But surely this will not do—and will ultimately prove as harmful as Scylla—for an obvious reason: Humans are animals, products, like every other twig on the tree of life, of billions of years of evolutionary history. It would be the most extraordinary happening in all intellectual history if the cardinal theory for understanding the biological origin and construction of our brains and bodies had no insights to offer to disciplines that study the social organizations arising from such evolved mental power. We may reject blinkered or inadequate accounts of human behavior (i.e., the part-by-part adaptationism of ultra-Darwinian sociobiology), and we should certainly combat proposed "partnership" by destruction and incorporation (the reduction of social sciences to evolutionary biology). But, surely, the struggle in social science must be to find and use a more adequate evolutionary biology, not to reject proffered aid and genuine partnership because certain previous proposals have been poisoned apples of temptation rather than pipes of

peace and shared feasts. This paper is really dedicated to a simple proposition in this vein—that such a partnership of mutual respect and enlightenment can be forged, and that the key intellectual instrument can be found in the concept of exaptation.

The Human Brain as a *Prima Facie* Case for Dominant Exaptation in the Radical Mode

The strict, or ultra-Darwinian, style of evolutionary argument grew in popularity during the 1940s and 1950s, and peaked in the international orgy of celebrations attending the centenary of the *Origin of Species* (and the sesquicentenary of Darwin's birth, for he published his greatest work conveniently at age 50 in 1859). As a main feature of this "hardening of the evolutionary synthesis" (as I have called this historical trend—see Gould, 1983, and affirmation of my thesis in Provine, 1986), reliance upon adaptationist explanations, to the near exclusion of everything else, became a watchword of evolutionary argument. This tendency culminated in sociobiology, and reached its caricatured hypertrophy (for all theories engender a dark side among uncritical acolytes) in speculative excesses of pop human sociobiology in the adaptationist mode (see Kitcher, 1985, for a critique).

But, since the 1970s, the main focus of evolutionary theory has begun to move in the opposite direction toward a critique of ultra-Darwinian narrowness and an expansion of concepts (with a retained Darwinian core). The two major themes of this expansion have a common thrust in revoking the hegemony of adaptationism and substituting a plurality of reasons for evolved forms and behaviors.

1. Levels and hierarchy. If natural selection works simultaneously on several levels of an ascending genealogical hierarchy, and if events at one level have effects at other levels by upward and downward causation (see Vrba & Gould, 1986), then phenomena at the organismic level need not be interpreted as Darwinian adaptations (the only available reading under ultra-Darwinism), for effects of other levels may also influence organismal phenotypes. Any feature promoting species selection by enhancing speciation rate will appear in more and more species of a clade (a branch of an evolutionary tree), but not for any advantage in the reproductive struggle among individuals. Any genetic element that can promote its own replication may provide several copies to the entire set of genes, with marked potential effects on evolution of the phenotype but without selection at the conventional Darwinian level of organismic struggle.

2. Constraints and channels. In the purest form of Darwinism, variation is raw material only—copious in amount, small in extent, and randomly distributed

in all directions about a modal form. Thus, all directional change occurs by natural selection, and all evolved forms may be interpreted as adaptations. Of course, no biologist has ever advocated total purity. Organisms are not congeries of atomized parts, each independent of all others. Adaptive change in one part entails correlated alteration of others, often for structural and developmental reasons unrelated to immediate adaptation. (Darwin took a great interest in this subject, which he called "correlation of growth.") The architecture of genetic and embryological systems sets channels of possible change. Selection may be required to push an organism down a channel, but the channel itself, though not an adaptation, acts as a major determinant of evolutionary direction. Above all, constraints of genealogy strictly limit the realm of conceivable adaptation (e.g., wheels might work well for locomotion, but organisms, built of physically connected parts, cannot fashion them).

No Darwinian has ever rejected the existence of constraints and channels. Rather, the conventional Darwinian argument denies them any important relative frequency in the production of phenotypes. Correlations exist, but can be broken by selection. Constraints occur, but powerful selection always finds a way (for example, even if a thumb must be built from a wrist bone, as when the panda's carnivorous heritage irretrievably altered its first digit to preclude opposability—Gould, 1980). The proper refutation of this argument must also invoke relative frequency—that is, by claiming high and irrevocable importance for the nonadaptations of channels and constraints. Exaptation provides a rationale for such an argument.

If we allow that revocation of adaptationist hegemony is a major reform of modern evolutionary theory, how does exaptation contribute—and how can this reform provide a more adequate evolutionary psychology? Of the two categories of exaptation, the second goes further in questioning adaptationist orthodoxy. In the first category, features evolved by natural selection for one purpose are coopted for another. This mode of exaptation breaks the false link of current utility with historical origin and, in doing so, refutes a great deal of muddled thinking that often passes for science in evolutionary reasoning about human origins. Thus, hands may be very good for throwing rocks, shooting arrows, and pressing triggers, but we may not infer that manipulability therefore arose as an adaptation for success in aggression. But this first mode of exaptation is not an argument against adaptationist hegemony because a feature's origin still resides in adaptation, and this mode speaks only of a shift in utility.

But in the second category—illustrated by delayed skull ossification and flying fish falling into water—presently useful characters did not arise as adaptations of all, but owe their origin to side consequences of other features (inevitable physical properties of mass for flying fish, an unknown reason for developmental delay of the cranium for ossification). In other words, the presently useful character (an aptation in our revised terminology) arose for nonadaptive reasons—

and the conventional Darwinian style of adaptationist argument cannot, in principle, resolve its origin. If exaptations of this second type are common, then classical Darwinism encounters a serious limit.

Spandrels

Gould and Lewontin (1979) have referred to these coopted nonadaptations as “spandrels,” borrowing an architectural term for spaces left over between structural elements of a building (e.g., the triangular space between the outer curve of an arch and the straight-sided walls and ceiling that bound the arch). Spandrels are not adaptations, but spaces left over following an architectural decision (which we may view as an analog of adaptation) to build with arches. But the bare spandrels are often ornamented later, and the chosen designs may fit the space with uncanny genius and beauty (e.g., four evangelists and four Biblical rivers in the four spandrels of the central dome in Venice’s Cathedral of San Marco in our “type” example—Gould & Lewontin, 1979). No one would argue that the spandrels exist to house the evangelists, no matter how good the fit. Yet lesser biological fits of form to function are often viewed as adequate evidence of adaptation.

Many Darwinian biologists had never considered the spandrels argument at all, and our choice of a clear (and ideologically neutral) architectural example did serve as a guide to comprehension and acceptance. But again, as with constraints and channels (see above), no cogent adaptationist rebuttal has ever denied the possibility or actuality of spandrels (which manifestly, after all, do exist). The sciences of natural history (and the social sciences as well) are domains of relative frequency, not (at least usually) of crucial experiments and single-case refutations based on laws of nature. The issue is not whether spandrels exist, but whether we encounter them frequently and whether they matter in the broad sweep of evolution. The adaptationist acknowledges their intelligibility, but constructs an argument to relegate them to a periphery of unimportance. (Nearly all arguments in evolutionary science proceed in this manner. Even for the most fundamental phenomenon of natural selection itself, no one has ever claimed exclusivity, but only predominant relative frequency. The main alternative, genetic drift, is inescapable in theory and undeniable in nature. The adaptationist ploy must argue for unimportance, not nonexistence—as in the classic claim that drift only occurs in tiny populations on the brink of extinction anyway.)

The adaptationist attack on spandrels therefore adopts the two classic strategies for winning an argument about relative frequency—what I call the “sequelae” and the “nooks and crannies” themes. The sequelae argument claims that spandrels only occur later and secondarily—as correlated consequences of a primary adaptation, never as active phenomena in themselves. To this I reply: (1) The claim is not always true (the weight of a flying fish just is; weight is not

secondary to or subordinately correlated with any adaptation). (2) The importance issue is not status at origin, but later evolutionary meaning; the last shall be first, and the correlated consequence may emerge as the directing feature. To say it one more time: Historical origin and current utility are different concepts.

The nooks and crannies argument holds that spandrels are just funny little spaces left over after adaptation sketches the major features of form and behavior. Again, I offer a twofold response: (1) Spandrels can be spatially extensive whatever their temporal status (the pendentive supports of a dome mounted on arches may cover more area than the dome itself). (2) The design and secondary utilization of spandrels may then feed back and determine major features of the entire structure. San Marco is a good example because mosaic decorations on the radially symmetrical central domes are designed in four-part symmetry, in clear harmony with the four pendentives below—so the form and number of spandrels determines the design of the “main” structure in this case.

The pro-spandrel arguments are clear enough in concept, but can we cash them out in practice? Can we locate important cases in which spandrels become more numerous and more important than the primary forms that generate them? If so, then the radical category of explanation—current utility based on original nonadaptation (“spandrels,” for an easier tag)—assumes great importance in evolution (and becomes much more than an interesting theoretical wrinkle in an abstract taxonomy of evolutionary possibilities).

The Human Brain

As the primary point of this paper, I wish to present an argument for regarding the human brain as, *prima facie*, the best available case for predominant exaptation—in other words, for a near certainty that exaptations must greatly exceed adaptations in number and importance (the proper criterion of relative frequency). Based on this argument, exaptation becomes a crucial concept for an evolutionary psychology. Much of our cultural tradition has been devoted to defining human uniqueness, particularly in terms of brain power and action. We may epitomize the evolutionary version of this massive interdisciplinary effort by stating that the human brain is, *par excellence*, the chief exemplar of exaptation.

The case can be best developed by recalling a famous episode from the history of evolutionary theory. Charles Darwin drew no boundaries in applying his theory of natural selection to organic nature. He specifically included the human brain—the structure that he had called “the citadel itself” in an early notebook—and he wrote two books (Darwin, 1871, 1872) on the evolution of human bodies, brains, and emotional expressions.

Alfred Russel Wallace, codiscoverer of natural selection, applied the theory (far more rigidly than Darwin, as we shall see) to everything else, but stopped

short at the human brain. Our intellect and morality, Wallace argued, could not be the result of natural evolution. Some higher power must have intervened to construct this latest and greatest of evolutionary innovations—natural selection for absolutely everything else; God for the human brain.

Darwin was aghast at his colleague's *volte face* right at the finish line itself. He wrote to Wallace in 1869: "I hope you have not murdered too completely your own and my child" (Marchant, 1916, p. 197). A month later, he added ruefully: "If you had not told me, I should have thought that [your remarks on the brain] had been added by some one else. As you expected, I differ grievously from you, and I am very sorry for it" (Marchant, 1916, p. 199). Wallace, sensitive to the rebuke, thereafter referred to his theory of the human brain as "my special heresy."

The outlines of this tale are well known, but the usual interpretation of Wallace's motives is not only wrong, but backwards. Sources cite Wallace's interest in spiritualism, or simply suggest intellectual cowardice in failing to extend an argument to its most threatening limit. I do not claim to have any insight into Wallace's psyche (where such factors may be relevant), but I can at least report that his explicit logical argument for cerebral uniqueness flowed not from reticence or active theological belief, but (ironically) from a fierce and opposite commitment to the exclusive power of natural selection as an evolution-agent.

Darwin viewed natural selection as a dominant but not exclusive force. Wallace, ironically, was the hyper-Darwinian of his age. He held that all forms and behaviors, including the most trivial, must be directly built by natural selection for utility. He wrote in 1867 (reprinted in Wallace, 1890):

No special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species, can exist but which must now be, or once have been, useful to the individuals or races which possess them.

Wallace would not admit the existence of spandrels, or of any nonadaptations correlated with features built by natural selection:

The assertion of "inutility" in the case of any organ is not, and can never be, the statement of a fact, but merely an expression of our ignorance of its purpose or origin.

Paradoxically, this very hyperadaptationism led Wallace to deny that natural selection could have built the human brain—for the following interesting and idiosyncratic reason. Wallace, almost uniquely among 19th-century Western natural scientists, was a genuine nonracist who believed in at least the near intellectual equality of all peoples. Yet he was a cultural chauvinist, who asserted a massive superiority of Western ways over "savage" practices. Consequently, under his hyperadaptationism, an insoluble paradox arises: natural selection can only build for immediate use; savages (surrogates for ancestors) have brains as

good as ours but do not employ them to nearly their full capacity in devising complex culture. Hence, natural selection did not construct the human brain.

To cite just one example, Wallace argued that the human ability to sing beautifully must have arisen long before any call upon this capacity, and cannot therefore be a product of natural selection. He wrote:

The habits of savages give no indication of how this faculty could have been developed by natural selection, because it is never required or used by them. The singing of savages is a more or less monotonous howling. . . . This wonderful power . . . only comes into play among civilized people. It seems as if the organ had been prepared in anticipation of the future progress in man, since it contains latent capacities which are useless to him in his earlier condition. (Wallace, 1895, p. 198)

Darwin was dumbfounded, primarily because he did understand the concept of spandrels (and also because he had more appreciation for the complexities of "savage" cultures). Wallace's illogic can be illustrated by the following anachronistic metaphor: If I put a computer in the business office of my small company, its capacities are not limited by the purposes of my installation. My computer, by virtue of its structural complexity and flexibility, maintains latent and unused capacities that must vastly outnumber the explicit reasons for my design or purchase. And the more complex the computing device, the greater the disparity between its field of potential and my explicit purposes (e.g., the calculator attached to my Casio watch may not perform much beyond my needs; but a Cray supercomputer can do more than I could ever even imagine).

Similarly for the evolution of the human brain. For the sake of argument, I will accept the most orthodox of Darwinian positions—that the human brain achieved its enlarged size and capacity by natural selection for some set of purposes in our ancestral state. Large size is therefore an adaptation. Does this mean that everything the enlarged brain can do must be a direct product of the natural selection that built the structure? Wallace certainly thought so, in arguing that "latent capacities" must imply preparation in "anticipation of future progress"—and therefore indicated intelligent design by God. But the principle of exaptation and the concept of spandrels expose Wallace's dilemma as a non-problem. Natural selection built the brain; yet, by virtue of structural complexities so engendered, the same brain can perform a plethora of tasks that may later become central to culture, but that are spandrels rather than targets of the original natural selection—singing Wagner (to cite Wallace's example, though some, even today, regard the *Ring* as monotonous howling), not to mention reading and writing.

Surely, for something so complex and so replete with latent capacity as the human brain, spandrels must vastly outnumber original reasons, and exaptations of the brain must greatly exceed adaptations by orders of magnitude. (The adaptations, moreover, are probably unidentifiable, given the limits of historical evidence about the ecological circumstances of human origins.) Surely, the cen-

tral traits of human culture, and the essences that define our concept of human nature, must arise more often as exaptations than as adaptations.

The concept of exaptation provides a one-line refutation of human sociobiology—and I do not regard such a statement as flippant or facetious. Sociobiology is an ultra-Darwinian theory based on adaptation. If, in principle, most culturally useful features of the brain are exaptations rather than adaptations, then they cannot be explained within the sociobiological research program without fatal revisions in its basic intent. A centrally functional feature of human culture or psychology, if it arises as a consequence of structural complexity and enters our explicit repertoire later by cooptation, cannot have a sociobiological explanation, whatever its current importance. At the very most, secondary adaptation might explain some aspects of current maintenance for the feature; but adaptation cannot, in principle, constitute the historical origin of a spandrel—and evolutionary studies are, preeminently, inquiries into origins. The human brain, as nature's most complex and flexible organ, throws up spandrels by the thousands for each conceivable adaptation in its initial evolutionary restructuring. What, then, by the criterion of relative frequency, is the best strategy for a useful evolutionary psychology—the sociobiology of strict Darwinism (which can only access the tiny proportion of adaptive traits), or a structural and correlational analysis that tries to map the spandrels of the brain's evolved capacity?

The Example of Religion

To choose just one overly broad and oversimplified example, much sociobiological effort has been expended in devising adaptive scenarios for the origin of religion (most center on the importance of tribal order and cohesion). But consider Freud's alternative, an argument based on spandrels. The origin of consciousness in our enlarged brain forced us to deal explicitly with the most frightening of all conceivable facts—the certainty of our personal mortality. To assuage this fear, we devised a great cultural variety of concepts with a central theme of mitigation—from metempsychosis (transmigration of souls), to resurrection of the body, to eternal realms for immaterial souls. These concepts form the core of religion as a cultural institution.

I am not so naive as to imagine that anything so complex and so multifaceted as religion could be fully rendered by either of these monistic propositions, but they do provide alternative approaches to a basis. The recognition of personal mortality is clearly a spandrel of our large brains, for surely no one would seek the adaptive advantage of increased brain size in achievement of this knowledge! If Freud is right, this focal and organizing concept of religion is a spandrel of a brain enlarged for other reasons; and religion did not arise as an adaptation (whatever its current function, and despite the cogency of a claim that all societies need institutions to promote and maintain group cohesion—for religion need not supply this function).

Go down the list of what you regard as human universals and cultural predictabilities. How many would you putatively assign to adaptation, and therefore view as amenable to sociobiological explanation? Incest avoidance? Such universal gestures as eyebrow flashing? Fine—but how long is your list and how much of our human essence, how much of what really makes culture, will you find? On the other side of the scale place the basis of religion as exaptation; add anything that relies on reading, writing, or any form of mental expression not in the initial repertoire of large-brained populations; add most of the fine and practical arts, the norms of commerce, the practices of war. Exaptation may be historically subsequent to adaptation, and may only coopt the structures and capacities built by adaptation. (But do not be so sure that the brain necessarily became large as an adaptation for more complex conceptualization; other alternatives exist, and consciousness itself may be exaptive.) No matter; the list of exaptations is a mountain to the adaptive molehill. Structural consequences have outstripped original bases. Human uniqueness, human power, human nature itself, lies in the consequences.

The Importance of Exaptation

Adaptation has been the canonical concept of English evolutionary thought, and of Darwinian traditions. The concept is easy to grasp, and it strikes a deep cultural resonance with a cardinal source of our solace—a cherished belief in the world's essential rightness. John Ray, in the late 17th century, and William Paley, in the early 19th, used the word to describe the exquisite natural design that implied both God's existence and benevolence; Darwin, in a sense, only changed the causal framework.

Adaptations also became canonical for their ease and lack of ambiguity in illustration—and iconography is a powerful source of bias. All textbooks present lovely photos of adaptations for their primary illustrations of evolution—for who can fail to grasp the meaning of a butterfly that looks like a dead leaf, or the streamlined form of a dolphin? This popularity of the concept leads to the false impression that adaptations dominate both in frequency and importance for evolutionary change.

In fact, most classical adaptations are small, immediate adjustments or dead-end specializations—e.g., peacocks' tails or elaborate antlers. Adaptations tend to be restrictive, at least with respect to evolutionary innovation. Vrba and I (1986) argued that the key to long-term macroevolutionary success lies in the concept of an "exaptive pool"—a range of cooptable potentials inherent in structures built for other reasons. Quirky and presently unemployed potential is often the key to evolutionary breakthroughs.

Consider some major events that made the evolution of complex human consciousness possible; all are exaptive. Chromosomes and their precise division in the process of meiosis gave us requisite variability through sexual recombina-

tion, but the provision of variation for evolutionary futures cannot have been the initial adaptive value of sex (Maynard Smith, 1978). Gene duplication, as argued previously, made complexity of organisms possible by freeing copies for change, but the multiple copies may have arisen by selection at the gene level, with no initial relationship to phenotypes at all. And, to jump to the most recent point and crux of this article, the major features of human mentality may be exaptive as nonselected structural products of a brain grown large for a small set of adaptive reasons.

The same principle applies when we consider the specific history of any lineage, including our own. Most major transitions are exaptations, not adaptations. Recent discoveries (Coates & Clack, 1990) on streamlined shapes and supernumerary digits indicate that the tetrapod limb originally evolved for locomotion in water, and was fortuitously cooptable for later life on land (Edwards, 1989). The retention of five digits by our quadrupedal mammalian ancestors (rather than specialized adaptive reduction to hoofs or pads) permitted a later and crucial flexibility in manipulation of tools by our hands (Jarvik, 1980). Stereoscopic vision probably arose for precision of locomotion in the three-dimensional world of trees (Jerison, 1973), not for the purposes so central to modern human life. For that matter, since primates always exceeded other mammals in relative brain size, initial enlargement of the brain could not have occurred in the service of what we now call consciousness.

The same argument reinforces my claim that evolutionary psychology should seek its basis in a concept of exaptation, not adaptation. Consider just a few random jottings in conclusion (this paper has been egotistical enough; I have preached to my colleagues in cognate fields, but I dare not claim a handle on the good examples. I only suggest to you who know the examples that their evolutionary meaning is likely to lie in exaptation).

Fundamental Institutions

Freud's exaptive argument for religion could be applied to most institutions equally distant from biological immediacy and equally rich in conceptual structure. (I would be more open to adaptive explanations for more explicitly biological traits shared with other related species lacking our cultural richness—e.g., facial gestures, behaviors of sexual and parent-child bonding. Yet, even here, a crucial role for exaptation must be considered. The genetic argument for adaptation in avoidance of incest is strong and plausibly supported by high relative frequencies of incest taboos in human cultures. But what learning rule do we follow in deciding whom to avoid in sexual relations? Experiments on quail and other animals hint that an abstract rule of "prefer close but not too close" may function as a general aesthetic principle in tetrapods. If so, avoidance of incest may be but one specific manifestation of the rule—with forms of xenophobia as

another example at the other pole. In this case, the rule itself may have some ancient adaptive basis, and incest avoidance may simply be a highly useful exaptive instantiation.)

Whatever one decides on the generality of religion itself, the exaptive basis of many specific religious practices seems clear. When I wrote my original paper on spandrels, I was struck by Harner's (1977) postulate that massive human sacrifice among the Aztecs arose as an adaptation to beef up the meat supply (as limbs of victims were consumed). E. O. Wilson (1978) then welcomed this example as a primary illustration of an adaptive and genetic predisposition for carnivory in humans. Harner's argument fails on several specific grounds (Ortiz de Montellano, 1978)—from the inefficiency of the human butchery (only three limbs per torso), to the availability of sufficient protein from other sources, to the key observation that only people of high status, who needed supplementary protein least, were allowed to eat sacrificial victims. But I was most intrigued by Harner's failure to consider the obvious exaptive alternative—that cultural practices arising for other reasons (and greatly extended as positive feedback raised the numbers of victims, almost surely to the point of cultural maladaptation) generated lots of bodies that were then available for consequent use. Why invert the explanatory chain and see a consequence (cannibalism) as the hidden source of the entire complex phenomenon? Yet this story almost became an early classic of sociobiology.

Fundamental Attributes

Those characteristics that we share with other closely related species are most likely to be conventional adaptations. (For example, I accept my colleague Steve Pinker's (1985) argument for the basic mechanics of the visual system, while rejecting his extensions to special properties of human consciousness.) But attributes unique to our species, and constituting the essence of what we call *human* consciousness, are likely to be exaptations by the arguments of the last section.

As an obvious prime candidate, consider the greatest and most contentious of all subjects embodying claims for our uniqueness: human language. The adaptationist and Darwinian tradition has long advocated a gradualistic continuationism—constructing scenarios that language “grew” from gestural and calling systems of other species; trying to teach chimpanzees the rudiments of human linguistic structure, etc. Noam Chomsky, on the other hand, has long advocated a position corresponding to the claim that language is an exaptation of brain structure. (Chomsky, who has rarely written anything about evolution, has not so framed his theory, but he does accept my argument as a proper translation of his views into the language of my field—Chomsky, personal communications.) Many adaptationists have so misunderstood Chomsky that they actually suspect

him of being an odd sort of closet creationist. For them, evolution means adaptive continuity, and they just cannot grasp the alternative of exaptive seizure of latent capacity that is present for other reasons.

The spectacular collapse of the chimp language experiments, and their exposure as some combination of wishful thinking and the Clever Hans effect, have made Chomsky's alternative all the more plausible. Cross-species continuity must exist, of course, in the growth of conceptual powers, but why should our idiosyncratic capacity for embodying much of this richness in the unique and highly peculiar mental structure called language be seen as an expression of this continuity? The traits that Chomsky (1986) attributes to language—universality of the generative grammar, lack of ontogeny (for language “grows” more like a programmed organ than like memorizing the kings of England), highly peculiar and decidedly nonoptimal structure, formal analogy to other attributes, including our unique numerical faculty with its concept of discrete infinity—fit far more easily with an exaptive, rather than an adaptive, explanation. The brain, in becoming large for whatever adaptive reasons, acquired a plethora of cooptable features. Why shouldn't the capacity for language be among them? Why not seize this possibility as something discrete at some later point in evolution, grafting upon it a range of conceptual capacities that achieve different expression in other species (and in our ancestry)?

Evolutionary Scenarios

Consider everyone's favorite game in evolutionary reconstruction—the spinning of behavioral and ecological scenarios for human origins. We usually consider these efforts as exercises in adaptationism. But, given the cardinal property of adaptation as usually limiting and restricting, and given the need to posit structures that permit flexibility and opportunity in conceptualizing human origins, these scenarios almost always make a claim for *exaptation* at crucial junctions (not, perhaps, in the radical mode of spandrels, but at least in the more conventional style of quirky functional shifts from an original reason to a very different consequence).

As just one example, recently subject to much discussion and debate, consider Falk's (1990) “radiator theory” (so close to Aristotle's old idea that the brain cools the blood). In her theory, gracile (slender) and robust (heavy-boned) australopithecines evolved different adaptations for adequate cranial blood flow in bipedal creatures—robusts via a greatly enlarged occipital/marginal sinus system, graciles via a widespread network of veins becoming more elaborate with time. This network system, an efficient cooling device, may have arisen as an adaptive response to the more intense solar radiation of savanna habitats favored by graciles. But this “radiator” then released a thermal constraint on brain size—allowing a larger brain to cool adequately. The graciles could evolve

into the large brained *Homo* lineage; the robusts were stuck. Thus, the radiator system, arising as an ecological adaptation in initially small-brained graciles, became an exaptation for cooling the enlarged brain of their descendants. If Falk is right, we would not be here today but for this crucial exaptation.

Current Utility

If you doubt all the other arguments for exaptation, just make a list of the most important current uses of consciousness. Start with reading, writing, and arithmetic. How many can even be plausibly rendered as adaptations?

Even so committed a hereditarian (and adaptationist) as Bouchard (of the Minnesota twin study) has seen the point, at least for the variability underlying human cognitive differences. Bouchard et al. (1990) write:

Whatever the ancient origins and functions of genetic variability, its repercussions in contemporary society are pervasive and important. A human species whose members did not vary genetically with respect to significant cognitive and motivational attributes . . . would have created a very different society than the one we know. (p. 228)

They even recognize that most of this variability, in ancestral contexts, might have been "evolutionary debris, unimportant to fitness and perhaps not expressed in prehistoric environments" (p. 228). Bravo, for this is a radical exaptive hypothesis with a vengeance (and almost surely correct)—describing a trait now vital to our social constitution, but so nonaptive at its origin that it achieved no phenotypic expression.

Yet just as these erstwhile adaptationists see the light, they retrogress with a knee-jerk assertion of the orthodox position that they denied in their primary specific interpretation!

Evolutionary psychologists or sociobiologists attempt to delineate species-typical proclivities or instincts and to understand the relevant evolutionary developments that took place in the Pleistocene epoch and were adaptive in the lives of tribal hunter-gatherers. The genes sing a prehistoric song that today should sometimes be resisted but which it would be foolish to ignore. (1990, p. 228)

And yet, the authors just told us that these particular genes probably were not singing at all back then, despite their crucial role in framing human society today. I interpret this inconsistency as a lovely example of working through the logic of a specific argument correctly (the claim for exaptation of a spandrel), but then missing the implication and spouting a contradictory orthodoxy. Clearly, we need to make the notion of exaptation explicit and available.

An evolutionary psychology properly grounded in the centrality of exaptation would be a very different, and less threatening, construct (for those feeling the breath of biological imperialism) than the conventional Darwinian account of continuity in adaptation, with its implications of gradualism, predictability, and

simple transfer from overt cultural expression to underlying biological basis. Exaptation, with its quirky and unpredictable functional shifts (e.g., thermoregulation to flight) and its recruitment of nonadaptive, even invisible structures (e.g., repeated copies of genes providing for future flexibility; the "debris" of unexpressed genetic variability leading to later cultural diversity), produces a cultural history with unanticipated changes in direction, potentially abrupt transitions, and no simply derived status of cultural expressions (for the path from biological substrate to overt manifestation passes through the switches of exaptive shift). The concept of exaptation honors the contingency of history, the unpredictable discontinuity of change in complex systems, and the plurality of legitimate sources of insight from biological substrate through quirky shift to social expression. We can therefore recall Haldane's dictum that "the universe is not only queerer than we suppose, but queerer than we *can* suppose." And lest we be tempted to read this (as Haldane most surely did not) as nihilism or pessimism (rather than as joy for being in such a fascinating place), we should also remember Einstein's equally famous remark that the Lord God is subtle, but not malicious (*Raffiniert ist der Herr Gott, aber boshaft ist er nicht*).

References

- Allmon, W. D. (in press). On the role of aptation in speciation. *Journal of Paleontology*.
- Blanc, M. (1990). *Les héritiers de Darwin*. Paris: Seuil.
- Bouchard, T. J., Lykken, D. T., McGue, M., Segal, N. L., Jr., & Tellegen, A. (1990). Sources of human psychological differences: The Minnesota study of twins reared apart. *Science*, 250, 223–228.
- Chatterton, B. D. E., & Speyer, S. E. (1989). Larval ecology, life history strategies, and patterns of extinction and survivorship among Ordovician trilobites. *Paleobiology*, 15, 118–132.
- Chomsky, N. (1986). *Knowledge of language: Its nature, origins, and use*. New York: Praeger.
- Coates, M. I., & Clack, J. A. (1990). Polydactyly in the earliest known tetrapod limbs. *Nature*, 347, 66–69.
- Darwin, C. (1859). *On the origin of species*. London: John Murray.
- Darwin, C. (1871). *The descent of man and selection in relation to sex*. London: John Murray.
- Darwin, C. (1872). *On the expression of the emotions in man and animals*. London: John Murray.
- Edwards, J. L. (1989). Two perspectives on the evolution of the tetrapod limb. *American Zoologist*, 29, 235–254.
- Endler, J. A., & McLellan, T. (1988). The processes of evolution: Toward a newer synthesis. *Annual Review of Ecological Systems*, 19, 395–421.
- Falk, D. (1990). Brain evolution in *Homo*: The "radiator" theory. *Behavioral and Brain Sciences*, 13, 333–381.
- Gans, C. (1988). Adaptation and the form-function relation. *American Zoologist*, 28, 681–697.
- Gould, S. J. (1980). *The panda's thumb*. New York: Norton.
- Gould, S. J. (1982). Darwinism and the expansion of evolutionary theory. *Science*, 216, 380–387.
- Gould, S. J. (1983). The hardening of the modern synthesis. In M. Greene (Ed.), *Dimensions of Darwinism* (pp. 71–93). Cambridge, U.K.: Cambridge University Press.
- Gould, S. J. (1989). A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. *Evolution*, 43, 516–539.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, B*, 205, 581–598.

- Gould, S. J., & Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, 8, 4–15.
- Hamilton, W. D. (1971). The genetical evolution of social behavior, I. In G. C. Williams (Ed.), *Group selection* (pp. 23–43). Chicago: Aldine. (Reprinted from *Journal of Theoretical Biology*, 1964, 7, 1–16)
- Harner, M. (1977). The ecological basis for Aztec sacrifice. *American Ethnologist*, 4, 117–135.
- Jarvik, E. (1980). *Basic structure and evolution of vertebrates*. New York: Academic Press.
- Jerison, H. J. (1973). *The evolution of the brain and intelligence*. New York: Academic Press.
- Kitcher, P. (1985). *Vaulting ambition: Sociobiology and the quest for human nature*. Cambridge, MA: MIT Press.
- Lewin, R. (1982). Adaptation can be a problem for evolutionists. *Science*, 216, 212–213.
- Marchant, J. (1916). *Alfred Russel Wallace: Letters and reminiscences*. New York: Harper.
- Maynard Smith, J. (1978). *The evolution of sex*. Cambridge, U.K.: Cambridge University Press.
- Ortiz de Montellano, B. R. (1978). Aztec cannibalism: An ecological necessity? *Science*, 200, 611–617.
- Owen, R. (1849). *On the nature of limbs*. London: Van Voorst.
- Pierce, C. L. (1988). Predation avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia*, 77, 81–90.
- Pinker, S. (1985). *Visual cognition*. Cambridge, MA: MIT Press.
- Provine, W. B. (1986). *Sewall Wright and evolutionary biology*. Chicago: University of Chicago Press.
- Vermeij, G. J. (1987). *Evolution and escalation*. Princeton, NJ: Princeton University Press.
- Vrba, E. S., & Gould, S. J. (1986). The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. *Paleobiology*, 12, 217–228.
- Wallace, A. R. (1890). *Darwinism*. London: Macmillan.
- Wallace, A. R. (1895). *Natural selection and tropical nature*. London: Macmillan.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.
- Wilson, E. O. (1975). *Sociobiology. The new synthesis*. Cambridge, MA: Harvard University Press.
- Wilson, E. O. (1978). *On human nature*. Cambridge, MA: Harvard University Press.

STEPHEN JAY GOULD is Professor of Geology and Alexander Agassiz Professor of Zoology at Harvard University. He is a paleontologist with primary interest in evolutionary theory and its history. His latest books are *Wonderful Life* (1989) and *Bully for Brontosaurus* (1991).