The exaptive excellence of spandrels as a term and prototype

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ABSTRACT In 1979, Lewontin and I borrowed the architectural term “spandrel” (using the pendentives of San Marco in Venice as an example) to designate the class of forms and spaces that arise as necessary byproducts of another decision in design, and not as adaptations for direct utility in themselves. This proposal has generated a large literature featuring two critiques: (i) the terminological claim that the spandrels of San Marco are not true spandrels at all and (ii) the conceptual claim that they are adaptations and not byproducts. The features of the San Marco pendentives that we explicitly defined as spandrel-properties—their necessary number (four) and shape (roughly triangular)—are inevitable architectural byproducts, whatever the structural attributes of the pendentives themselves. The term spandrel may be extended from its particular architectural use for two-dimensional byproducts to the generality of “spaces left over,” a definition that properly includes the San Marco pendentives. Evolutionary biology needs such an explicit term for features arising as byproducts, rather than adaptations, whatever their subsequent exaptive utility. The concept of biological spandrels—including the examples here given of masculinized genitalia in female hyenas, exaptive use of an umbilicus as a brooding chamber by snails, the shoulder hump of the giant Irish deer, and several key features of human mentality—anchors the critique of overreliance upon adaptive scenarios in evolutionary explanation. Causes of historical origin must always be separated from current utilities; their conflation has seriously hampered the evolutionary analysis of form in the history of life.

Much Ado About Little and Lots

Just as the four evangelists fit so splendidly—but so obviously secondarily and epiphenomenally—into the spandrels of San Marco, I have been delighted beyond all measure by the unintended consequences spawned by our metaphor and example (1). Lewontin and I (1) designed this architectural analog as an illustration of dangers and fallacies in overzealous commitment to adaptationist explanations—and the notoriety of our paper surely testifies to the success of this primary intent.

But, my goodness, we never anticipated so many exaptive spinoffs from this introductory image—including (i) an entire book by linguistic scholars on our (mostly unconscious) literary tactics (2); (ii), a wise commentary by a noted scholar of medieval building (3); and (iii), wonder of wonders in our own field. Lewontin and I (1) invoked the principle of spandrels to introduce our critique of adaptationist logic because, in our judgment, the primary fallacy of this approach lies in a tendency to treat a proven current utility for any individual feature as prima facie evidence of its adaptive origin. We wished, in contrast, to emphasize that any adaptive change in a complex and integrated organism must engender an automatic (and often substantial) set of architectural byproducts. These sequelae—spandrels in our terminology—arise non-adaptively as secondary consequences [“correlations of growth” in Darwin’s phrase (19)], but then become available for later cooptation to useful function in the subsequent history of an evolutionary lineage. We began our article with an architectural, rather than a biological, example (a good architectural, rather than a distant discipline would evoke no a priori preference and could therefore be judged more fairly and without prejudice. I chose the mosaic decoration of the pendentives under the great dome of San Marco in Venice in part because I had been so impressed by their beauty and felt so instructed by the analogical transfer thereby suggested to issues of adaptation in my own field. I also thought that the architectural term “spandrel” could serve as an excellent label, fully applicable to biological examples, for the general phenomenon thus illustrated. I liked the term, first of all, because its etymological origin lay so firmly in the domain of measurement and geometry that D’Arcy Thompson had emphasized in his locus classicus [On Growth and Form (31), first published in 1917 and continually in print ever since] for the formalist critique of adaptationism—for the word spandrel arose as a diminutive offshoot from the most organic of all quantifications, the “span,” or distance, between the outstretched thumb and last finger. [Isaiah’s God shows his love for humanity by such solicitude in measurement: for he “who hath measured the waters in the hollow of his hand, and meted out heaven with the span” shall also “feed his flock like a shepherd” and “gather the lambs with his arm” (Isaiah 40:11–12)].

In architecture, the prototypical spandrel is the triangular space “left over” on top, when a rectangular wall is pierced by a passageway capped with a rounded arch (see Fig. 1). By extension, a spandrel is any geometric configuration of space inevitably left over as a consequence of other architectural decisions. Thus, the space between the floor and the first step of a staircase or the horizontal course between the lintels of a horizontal line of windows and the bottom of the row of windows on the floor just above are also called spandrels. By generalization then—and here I saw the utility of an application to problems of adaptation in biology—a spandrel is any

Spaniels of St. Marx.” Ouch! (5–6). The shrill and negative commentaries in the third and last category advance two claims against our example—one almost risibly trivial (that our spandrels aren’t spandrels), the other seriously false and based on a misreading of our clearly stated intent (that San Marco’s spandrels are adaptations after all).

Claim One: What’s In A Name?

Lewontin and I (1) invoked the principle of spandrels to introduce our critique of adaptationist logic because, in our judgment, the primary fallacy of this approach lies in a tendency to treat a proven current utility for any individual feature as prima facie evidence of its adaptive origin. We wished, in contrast, to emphasize that any adaptive change in a complex and integrated organism must engender an automatic (and often substantial) set of architectural byproducts. These sequelae—spandrels in our terminology—arise non-adaptively as secondary consequences [“correlations of growth” in Darwin’s phrase (19)], but then become available for later cooptation to useful function in the subsequent history of an evolutionary lineage. We began our article with an architectural, rather than a biological, example (a good architectural, rather than a distant discipline would evoke no a priori preference and could therefore be judged more fairly and without prejudice. I chose the mosaic decoration of the pendentives under the great dome of San Marco in Venice in part because I had been so impressed by their beauty and felt so instructed by the analogical transfer thereby suggested to issues of adaptation in my own field. I also thought that the architectural term “spandrel” could serve as an excellent label, fully applicable to biological examples, for the general phenomenon thus illustrated. I liked the term, first of all, because its etymological origin lay so firmly in the domain of measurement and geometry that D’Arcy Thompson had emphasized in his locus classicus [On Growth and Form (31), first published in 1917 and continually in print ever since] for the formalist critique of adaptationism—for the word spandrel arose as a diminutive offshoot from the most organic of all quantifications, the “span,” or distance, between the outstretched thumb and last finger. [Isaiah’s God shows his love for humanity by such solicitude in measurement: for he “who hath measured the waters in the hollow of his hand, and meted out heaven with the span” shall also “feed his flock like a shepherd” and “gather the lambs with his arm” (Isaiah 40:11–12)].

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Spanish...
space necessarily and predictably shaped in a certain way, and
not explicitly designed as such, but rather arising as an
inevitable side consequence of another architectural decision
(to pierce a wall with a rounded arch, to build a stair at a
certain height from the floor, to construct a multistoried
building with windows in rows). I believed that this concept—a
predictable form that arises as a side consequence rather than
a direct adaptation—had important application to biology but
lacked a name. (Darwin’s “correlation of growth” came to
mind, but his term is ambiguous and never caught on in any
case.) I thought, and continue to feel, that spandrel is the most
obvious, the most useful, and the most historically sanctioned
term available for such a central concept.

Moreover, the term spandrel is particularly applicable to
biological problems of adaptation because the architectural
concept stresses the same point of distinction between histor-
ical origin and later utility that has proven so troublesome in
evolutionary theory. Architectural usage has always empha-
sized the availability of these left-over spaces for later deco-
ration that may come to define the beauty or essence of a style.
(I grew up in New York City and always appreciated the
elaborate geometrical ornamentations on the panels that cover
the horizontal spandrel-courses of our numerous Art Deco
buildings.) For example, Webster’s Third New International
Dictionary (32) gives these two subsidiary definitions for
spandrel: “an ornamentaly treated space between the... . . .
curve of an arch and an enclosing right angle” and “a
corner space with scroll work or other decorative filling
between a rounded corner... and a squared corner of a
rectangular frame.” Thus, the definition of a spandrel includes
both its origin as a necessary but consequential (and therefore
“nonadaptive”) form and its availability for later (or second-
adaptively, and potentially crucial, use—the two concepts
that permit a fruitful application to evolutionary biology.

The nonconceptual, purely terminological, and truly trivial
issue that seems to bother Dennett (4) and Houston (7) so
much involves my application of the term spandrel (classically
used, as shown in Fig. 1, for two-dimensional spaces left over)
to the three-dimensional tapering triangular spaces between
the round domes and the four rounded arches that support
each dome in the cathedral of San Marco in Venice. These
spaces—necessarily four in number and necessarily tapering
and triangular, when domes are mounted on four arches joined
at right angles (see Fig. 1)—are called “pendentives.” [And, for
what it’s worth, I knew this before Lewontin and I ever wrote
our original article in 1979 (1)—not because I have any
extension to three dimensions (and therefore to full
generality), a usage also sanctioned by some architectural
historians, seems well justified, both by tradition and for the
claim (ref. 1, p. 339) about the nonadaptive, and architecturally
active role of pendentives in buttressing) stresses the same
point of distinction between historical origin and later utility—
the architectural term spandrel seems eminently (may I even
say optimally) suited. For spandrel does enjoy standard use, at
least for two-dimensional spaces that originate as byproducts.

Thus, if evolutionary biology needs a general name for the
concept of a nonadaptive architectural byproduct of definite
and necessary form—a structure of predictable size and shape
that then becomes available for later and secondary utility—
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The extension to three dimensions (and therefore to full
generality), a usage also sanctioned by some architectural
historians, seems well justified, both by tradition and for the
clear benefits always conferred by a generalized descriptor for
an important concept in any scientific field.

Claim Two: Are Spandrels Spandrels or Adaptations?

In arguing that the San Marco pendentives possess some
structural utility (7), or in claiming that they must have been
actively chosen as a design solution (4) (and must therefore be,
at least by analogy, adaptive) because unused alternatives exist
in principle (squinges instead of pendentives, various forms of
bracketing rather than smooth spaces suited for mosaics), our
critics have either ignored or misunderstood our clearly stated
claim (ref. 1, p. 339) about the nonadaptive, and architecturally
consequential, aspect of these spaces. We never thought or
argued that the pendentives do nothing useful. (In some trivial
sense, for starters, they work much better than similar spaces
left open and unroofed, if only because they keep out the rain.)
Robert Mark (3), the distinguished civil engineer and archi-
tectural historian who analyzed our debate with Dennett (4)
and who affirms our central claim about the necessary form
and number of spandrels as byproducts (while also noting the
active role of pendentives in buttressing) stresses the same
point in recognizing the inevitably diamond-shaped form and
even spacing of the ceiling spandrels in King’s College Chapel

![Fig. 1. (Upper) A pendentive (or three-dimensional spandrel) formed as a necessarily triangular space where a round dome meets
two rounded arches at right angles. (Lower) “Classical” two-
dimensional spandrels; the necessarily triangular spaces between
rounded arches and the rectangular frame of surrounding walls and
ceilings.

I will leave it to professional architects to decide whether the
general concept of a spandrel as a two-dimensional byproduct
of definite form should be extended to such three-dimensional
analogues as the pendentives of San Marco or the diamond-
shaped panels that must be present at the intersections of the
fans in any late gothic fan-vaulted ceiling (our other example
in ref. 1). I agree with Dennett and Houston that most
architects, apparently, do not do so. But many do, particularly
in continental European usage. In our original paper (1), I
followed Bacchion (8), who discusses the San Marco penden-
tives under the general term spandrel: “In the spandrels, under
the Evangelists, there is an extraordinary group: four men
pouring water from leather bottles on their shoulders.” This
usage seems general. Franchi (9), for example, identifies as
spandrels the famous pendentives under the dome of the Pazzi
Chapel at the Church of Santa Croce in Florence (the burial
place of Galileo), where Brunelleschi also placed figures (in
terra cotta) of the evangelists: “In the spandrels between the
dome and the arches there are the four evangelists attributed
to Brunelleschi himself.”]
ceiling spandrels between the fan vaults in King's College. For our second example, the diamond-shaped corners, between the upper sides of the arches and the base of the dome. Whatever their coordinated utility in the original structure, Spandrels may keep out the rain, protect privacy, exclude birds, cut down noise, even help to buttress the building—but their availability for later fruitful use (the main point of our example from the start and surely not a weakness in our argument) and whatever their coordinated utility in the original structure. Spandrels may keep out the rain, protect privacy, exclude birds, cut down noise, even help to buttress the building—but their basic physical features of size, shape, and number originate as secondary consequences, not primary intents.

Standard Arguments Against Spandrels and the Excellence of San Marco as a Prototype

The testable and fruitful application of our definition of spandrels to biological evolution requires that two standard objections be overcome. Lewontin and I ventured outside our field and chose the pendentives of San Marco as our primary illustration because this case provides a wealth of historical and structural data (not always available in the imperfect archives of evolutionary sequences) sufficient to rebut both major arguments against the importance and utility of the concept of spandrels.

Separating Primary Cause (Adaptation) from Secondary Effect (Spandrel). Spandrels are architecturally enforced byproducts of primary changes. But spandrels may then be subsequently coopted for highly fruitful use—leading to the result that Gould and Vrba (10) called exaptation. But if we now have available only the modern structure with its mix of primary adaptations and secondarily exapted spandrels—the usual situation in biology when we do not have a fossil record of actual historical stages leading to a present structure—then how can we identify and allocate the proper statuses? After all, both types of features may now be exquisitely well "crafted" for a current utility—for the exapted spandrel may work just as well, and may be just as crucial to current function of the whole, as the primary adaptation. That is, the central dome of San Marco now sits on rounded arches with excellent structural integrity, but the evangelists fill the spandrels with equally excellent design for a central iconographic purpose. So which of other architectural decisions and therefore nonadaptive in their origin. Spandrels are not adaptations, despite their availability for later fruitful use (the main point of our example from the start and surely not a weakness in our argument) and whatever their coordinated utility in the original structure. Spandrels may keep out the rain, protect privacy, exclude birds, cut down noise, even help to buttress the building—but their basic physical features of size, shape, and number originate as secondary consequences, not primary intents.

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architects to provide the four pendentives so that they could execute their evangelical design.

In principle, two basic methods—one better than the other—can resolve this crucial question of causal sequence. First (and evidently superior for relying on raw observation rather than inference), we might obtain evidence for an actual historical order and therefore be able to know which feature arose first as a primary adaptation and which subsequently as a coopted byproduct. Second (and more generally applicable in relying on available data of present cases, but necessarily inferential), we may tabulate the “comparative anatomy” of current examples in a cladistic context and try to determine a historical order from the distribution. For example, all snails that grow by coiling a tube around an axis must generate a cylindrical space along the axis. This space is called an umbilicus. It may be narrow and entirely filled with calcite (then called a columella), but it is more often, and especially in land snails, left open. A few species use the open umbilicus as a brooding chamber to protect the eggs (11).

We may therefore ask: Is the umbilical brooding chamber a coopted spandrel—a space that arose as a nonadaptive, geometric byproduct of winding a tube around an axis? Or did snails initially evolve their spiral coiling as part of an actively selected design centered upon the direct advantages of protecting eggs in a cigar-shaped central space? We cannot use the first method of actual historical sequence to resolve this question because we do not know whether the first coiled snails brooded their eggs in an umbilical chamber. But the second method of comparative anatomy seems decisive in this case, however inferential: The cladogram of gastropods includes thousands of species, all with umbilical spaces (often filled as a solid columella and therefore unavailable for brooding) but only a very few with umbilical brooding. Moreover, the umbilical brooders occupy only a few tips on distinct and later-arising twigs of the cladogram, not a central position near the root of the tree. We must therefore conclude—both from geometric logic (ineluctable production of the umbilicus, given coiling of the shell) and from the distribution of umbilical brooding on the cladogram—that the umbilical space arose as a spandrel and then became coopted for later utility in a few lines of brooders.

This case is admittedly a bit simplistic in its obvious and unambiguous resolution. But many actual examples in biology do not resolve easily by this second method because the putative spandrel is not so clearly consequential as a structure, or so taxonomically restricted as an evolved feature, that an inference of historical order evidently follows. For example, did the famous “female-mimicking” genitalia of the female spotted hyena (12–14) arise as a spandrel of the evolution of female dominance and superior size (an adaptation built by high testosterone titers, which induce masculinized genitalia as an automatic result) or did masculinized genitalia, as a direct adaptation produced by natural selection on endocrine levels, yield aggressivity and large female size (an adaptation produced by coopting a byproduct)? Many details of this case strongly favor the interpretation of masculinized genitalia as a spandrel (14). But resolution requires a wealth of information often not available, and does not follow so clearly from the logic of the case, as for the previous example of snail umbilici.

The instructive power of the San Marco prototype lies in a clear weight of evidence provided in both categories. First, in happy contrast with most biological examples, in which long geological histories and imperfect evidence often preclude resolution, we know the actual timing of construction in San Marco and can clearly identify the pendentives as secondary spandrels with respect to their optimal number and form for housing evangelists. The domes of San Marco, and all accompanying structures, were built three centuries before the mosaicists placed their design of such excellent fit into the pendentives (15).

The second criterion of comparative anatomy also indicates that the form and number of pendentives originated as a nonadaptive byproduct. Thousands of Western buildings feature domes atop rounded arches—and every single one of them generates tapering triangular spaces at the intersections. These pendentives are not adapted, but a side result of which each appropriate to the local circumstance, whereas many are not ornamented at all (indicating that pendentives must be generated but need not bear “adaptive” designs). I have seen various religious foursomes in the pendentives of other churches—the four major Old Testament prophets, Isaiah, Jeremiah, Ezekiel, and Daniel; or, in San Ignazio in Rome (and “politically correct” by current standards of gender equality), four Old Testament heroes and their weapons: David with his sling, Judith with her sword (to behead Holophernes), Samson with his jawbone, and Jael with her tentpost (to transfix Sisera through the head). I also have noted secular themes in civic or scientific building—the four continents of Africa, Europe, Asia, and America under the main dome of the Victor Emanuel arcade in Milan; four classical lawmakers (Justinian, Pericles, Solon, and Cicero) under the glass dome in the Victorian courtroom of the Landmark Center, St. Paul, MN; four mainstays of civilization (peace, justice, industry, and agriculture) in the County Arcade of Leeds, England, built in 1900; or the four Greek elements in the pendentives under the main dome at the headquarters of the National Academy of Sciences in Washington, DC, the publishers of this journal! St. Paul’s Cathedral in London mounts the central dome on eight arches, and the eight resulting pendentives feature the four evangelists at the eastern end, contrasting with the four great Old Testament prophets to the west.

Even more persuasively, the chosen foursomes for ornamentation sometimes seem rather forced or even ill-fitting, thus indicating that the fixed number of spaces (and their form) precede any decision about embellishment. In the 16th century church of San Fedele in Milan, for example, four concepts, personified as women, decorate the spandrels under the central dome—the famous biblical trio of faith, hope, and charity (1 Corinthians, chapter 13), with the remaining fourth spandrel occupied by religion. Three spandrels might have carried the intended design better, but architectural constraint dictated a quartet, so the designers had to draft a fourth participant, however unsanctioned by a very famous quotation. Thus, after noting such diversity of fitting design, or often no design at all, we can scarcely conclude that such a range of disparate reasons (or no evident reason at all) invariably engenders the same structural decision—that a building should be made with pendentives to secure a substrate for a chosen decoration. The pendentives must therefore originate as geometrically constrained byproducts of a decision to mount domes on arches—and must acquire, only later and consequently, their utility as a fitting space for a meaningful design.

Two False Claims for the Insignificance of Spandrels. The prototype example of San Marco’s pendentives provides clear refutation for two standard denigrations of the importance of spandrels (the fallback position of opponents, following an admission that spandrels exist and can be identified from comparative and historical data).

The Argument of “Nooks and Crannies.” Spandrels may undeniably arise as unintended consequences of any adaptation, but if such sequences only include truly tiny and meaningless bits and pieces lying in the nooks and crannies of a primary structure—as in the mold marks on a bottle, for example—then spandrels exist but do not matter. To rebut this claim, we must recognize that consequential does not mean small or unimportant. Spandrels can be as prominent as primary adaptations. The area covered by the four pendentives under any dome in San Marco does not differ much from the
The Argument That Secondary Means Unimportant. The failure to separate reasons for historical origin from realities of current utility underlies many fallacies in evolutionary thought about adaptation (10,16). (Indeed, the chief mistake about spandrels—the false inference of adaptive initiation from observation of current fitness, as in assuming that San Marco’s pendentives were built to house the evangelists—arises from this erroneous argument.) This second invalid denigration of spandrels invokes the same error, as critics argue that spandrels, because they arise secondarily as consequences, can never be important components of a structural design. But manner of origin bears no necessary relationship to the extent or vitality of a later coopted role.

The pendentives of San Marco expose this fallacy particularly well—a major reason for my initial choice of this example. Extensive feedback from the pendentives to the mosaics of the dome proves that secondary features can exert pervasive influence upon the basic design of a totality. The domes of San Marco are radically symmetrical and therefore induce, in se and considered alone, no reason for favoring a quadrupartite mosaic design. Yet all but one of San Marco’s five domes contain mosaics arranged in four-part symmetry—clearly, in each case, to harmonize with the iconography in the four triangular spandrels below. Lewontin and I began our 1979 paper with this observation (ref. l, p. 339):

The great central dome of St. Mark’s Cathedral in Venice presents in its mosaic design a detailed iconography expressing the mainstays of Christian faith. Three circles of figures radiate out from a central image of Christ: angels, disciples, and virtues. Each circle is radially symmetrical in structure. Each quadrant meets one of the four spandrels in the arches below the dome.

Another dome contains angels in the pendentives and the twelve apostles in the dome, arranged in four groups of three, with each group clearly centered on one of the four pendentives below. Yet another dome presents four male saints in the dome and four female saints in the spandrels, with each male perfectly centered between two of the females. Thus, an ineluctable architectural byproduct can, nonetheless, determ ine the fundamental design of a totality—clearly, in each case, to harmonize with the iconography in the four triangular spandrels below. Lewontin and I began our 1979 paper with this observation (ref. l, p. 339):

The centrality of the principle of spandrels in evolutionary thought

The logical and empirical separation of current utility from historical origin has been a mainstay of proper and subtle adaptationist argument from Darwin’s time to our own—whereas a failure to recognize this necessary division, and to make conjectural inferences about initial reasons from information about contemporary fitness alone has been, and continues to be, the bugbear and defining error of naive or simplistically fundamentalist ultra-Darwinism (17, 18), a dubious approach that features the invention of what Lewontin and I have called (1), following Kipling’s lead, ”just-so” stories about ultimate reasons for the origin of odd structures and behaviors.

In the classic example of proper separation, Darwin (19) invoked the principle of functional shift to rebut Mivart’s famous argument (20) that continuous evolution could not account for “the incipient stages of useful structures.” If the earliest stages in the evolution of a wing, for example, offer no conceivable benefit in flight, then these incipient structures must have performed some other primary function and been coopted later (and at more elaborate form) for aerodynamic benefit. Darwin (ref. 19, p. 138) speaks of “the highly important fact that an organ originally constructed for one purpose . . . may be converted into one for a widely different purpose.”

This principle of quirky and unpredictable functional shift underlies much of evolution’s contingency (21) but does not alter or broaden the adaptationist paradigm because structures still arise by selection, and for utility—albeit for a different function than homologs in modern descendants now perform. The principle of spandrels provides a more radical version of cooption “for a widely different purpose” because the expected structure originated as a byproduct and not as an explicit adaptation at all. Therefore, structures that may later become crucial to the fitness of large and successful clades may arise nonadaptively (whatever their subsequent, coopted utility)—and the principle of adaptation cannot therefore enjoy the near ubiquity that strict Darwinians wish to impute.

Because multicellular organisms are structurally complex and built of many integrated parts, any primary adaptation must generate a set of architecturally enjoined side consequences, or spandrels. The number and complexity of these spandrels should increase with the intricacy of the organism under consideration. In some region within a spectrum of rising complexity, the number and importance of usable and significant spandrels will probably exceed the evolutionary import of the primary adaptation.

Some spandrels arise as simple geometric consequences, expressed in basic dimensions of size and shape. These features may become important to the life of descendant organisms, but their range of cooptable utility may be small. The simple cylindrical tube of a snail’s umbilicus may encompass few potential uses beyond protection of a brood. Similarly, the broadly raised area at the withers of the giant Irish deer (Megaloceros giganteus)—a spandrel produced by necessary elongation of the neural spines of the vertebræ for insertion of a strong ligamentum nuchae to hold up the massive head of this maximally horned deer (22, 23)—may become enlarged, altered in shape to a more prominent and localized hump, and festooned with distinctive colors, all (presumably) for coopted function in mating display. But the potential of such bumps and spaces may be limited and may never exceed the primary adaptation (which originally engendered the feature in question as a spandrel) in evolutionary importance. (This case is particularly interesting because we only know about the unfossilizable hump, not to mention its coloration, from the cave paintings of our Cro-Magnon ancestors.)

A more diverse, and more widely cooptable, set of spandrels may emerge from extensive developmental consequences of adaptive changes, particularly in animals with complex embryologies. The masculinized genitalia of the female spotted hyena, as discussed previously, provide a classical example and a subject of much recent literature (12–14). Many puzzles of human form and behavior—often subjects of intense debate, or even sources of much anguish and psychic pain (including Freud’s anatomically impossible argument that women, to avoid frigidity, must switch from a clitoral to a vaginal site for orgasm)—can be resolved by recognizing that the adaptations of one sex (female breasts or the penile site of male orgasm) may be converted into those of the other, thanks to common pathways of development [the nonfunctional nipples of males or the clitoral site of female orgasm, perfectly satisfactory for sexual pleasure but divorced from the Darwinian summum bonum of enhanced reproductive success, (refs. 24–26)].

In a third domain of maximal expression for spandrels vs. primary adaptations, organs of extreme complexity must in-
clude capacities for cooptation that can exceed, or even overwhelm, the primary adaptation. The chief example in biology may be a unique feature of only one species, but we obviously (and properly) care for legitimate reasons of parochial concern. The human brain may have reached its current size by ordinary adaptive processes keyed to specific benefits of more complex mentalities for our hunter-gatherer ancestors on the African savannahs. But the implicit spandrels in an organ of such complexity must exceed the overt functional reasons for its origin. (Just consider the obvious analogy to much less powerful computers. I may buy my home computer only for word processing and keeping the family spreadsheet, but the machine, by virtue of its requisite internal complexity, can also perform computational tasks exceeding by orders of magnitude the items of my original intentions—the primary adaptations, if you will—in purchasing the device).

Thus, in analyzing the evolutionary basis of features now crucial to the functional success of organisms, we must learn to appreciate the range of potential reasons for the origin of such traits. The biases of strict Darwinism often narrow our focus to adaptive bases for all aspects of a feature’s evolutionary history—so that the primary mechanism of natural selection may be viewed as a direct causal basis for the entire sequence, whatever shifts of function may occur. However, and perhaps ironically, we must recognize that complexities of structure and development clearly impose a set of attendant sequelae upon any adaptive change. These sequelae—spandrels in the terminology of this paper—arise nonadaptively as architectural byproducts but may regulate, and even dominate, the later history of a lineage as a result of their capacity for cooptation to subsequent (and evolutionarily crucial) utility. (Or they may continue as nonadaptive spandrels and still remain important as features central to our understanding and analysis of organic form in evolution.)

A failure to appreciate the central role of spandrels, and the general importance of nonadaptation in the origin of evolutionary novelties, has been the principal impediment in efforts to construct a proper evolutionary theory for the biological basis of universal traits in *Homo sapiens*—or what our vernacular language calls “human nature.” Promoters of the importance of spandrels, and of nonadaptation in general, are not trying to derail the effort to establish a true “evolutionary psychology” on genuine Darwinian principles (rather than the limited hyperadaptationist doctrine that currently uses this label; see refs. 27–29 for exposition and ref. 17 for a critique), or even to overthrow the centrality of adaptation in evolutionary theory. We wish, rather, to enrich evolutionary theory by a proper appreciation of the interaction between structural channeling (including the nonadaptive origin of spandrels as a central theme) and functional adaptation (as conventionally analyzed in studies of natural selection) for generating the totality and historically contingent complexity of organic form and behavior.