

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 faintly philistine (and avowedly secular) professional community (4–7), a burgeoning interest in at least two humanistic subjects generally shunned by scientists for reasons of passive ignorance, or even active distaste: church architecture and literary parody [of the puerile, “ain’t-I-clever,” sort embodied in two recent titles, “The Scandals of San Marco” and “The

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 cooption 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 decision as validated by the intensity of ensuing discussion) because we believed that adaptationist bias would cloud the logic of an illustration “too close to home” whereas a case from 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

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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 historical origin and later utility that has proven so troublesome in evolutionary theory. Architectural usage has always emphasized the availability of these left-over spaces for later decoration 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 ornamentally 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 secondarily adaptive), 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 extensive expertise in architectural terminology, but because I asked my friend Peter Stevens, a distinguished Boston architect and author of a fine modern work in the tradition of D’Arcy Thompson, *Patterns in Nature* (33)].

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 analogs 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 pendentives 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.”

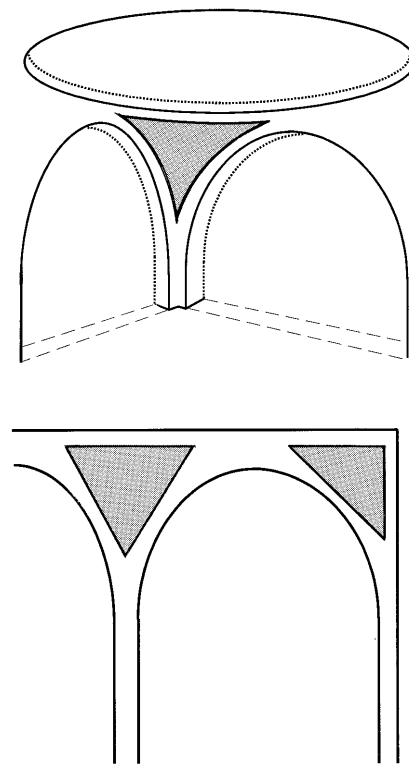


FIG. 1. (Upper) A pendentive (or three-dimensional spandrel) formed as a necessarily triangular space where a round dome meets two rounded arches at right angles. (Lower) “Classical” two-dimensional spandrels; the necessarily triangular spaces between rounded arches and the rectangular frame of surrounding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

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—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. 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 (squanches 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 architectural 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

(our second example in ref. 1) but then stating that closed rather than open spandrels operate “to prevent the spread of fire, to improve acoustics and to exclude birds in the roof from entering the chapel” (ref. 3, p. 385).

By spandrel, Lewontin and I (1) intended (purposefully and specifically) to designate the physical properties—form, position, constitution, and number, for example—that must arise as enforced consequences of primary reasons for building or altering a complex structure. (We assume that, in biological systems, the usual primary reason will center upon the standard mechanism of natural selection leading to adaptive change.) In San Marco, the primary decision—surely “adaptive” by analogy, because architects chose this option based on known prior success—involved mounting domes on four rounded arches meeting at right angles. Once this solution has been chosen, the two spandrel-properties (inevitable byproducts) of the pendentives necessarily follow: the pendentives must be four in number, and each must have a tapering triangular form, widest at the top, and narrowing to the slit between the two arches below their circular tops. Whatever the function of the pendentives, ranging from relatively trivial in keeping out the rain to potentially vital in buttressing the dome, their number (four) and their form (roughly triangular) arise as inevitable byproducts of the primary decision to mount domes on arches. This is the property of consequential necessity that we wanted to capture in our general definition of a spandrel. We wrote in the first paragraph of our article (1):

Spandrels—the tapering triangular spaces formed by the intersection of two rounded arches at right angles—are necessary architectural byproducts of mounting a dome on rounded arches. . . . The system begins with an architectural constraint: the necessary four spandrels and their tapering triangular form. (p. 339)

We wanted to emphasize this nonadaptive origin for basic properties of spandrel-spaces because biologists so often err in inferring an adaptive origin from a later and fruitful use of available spandrels. Again, the San Marco example seemed particularly instructive, for the form and number of the spandrels arose as nonadaptive byproducts but, some three centuries later, these spaces were ornamented with beautiful mosaics in a particularly fitting way. For the central dome, the mosaicists placed the four evangelists at the tops of the spandrels, with the four Biblical rivers (of *Genesis*, chapter 2) just below, each personified as a man pouring water into the narrow space at the spandrel’s bottom, where the flow irrigates a single flower. The design “fits” so well into the spandrel that, if we didn’t know the historical order of formation or appreciate the structural consequences of mounting domes on arches, we might invert causality and assume that the spandrels were designed explicitly to house the evangelists. We wrote (1):

Each spandrel contains a design admirably fitted into its tapering space. . . . The design is so elaborate, harmonious, and purposeful that we are tempted to view it as the starting point of any analysis, as the cause in some sense of the surrounding architecture. But this would invert the proper path of analysis. The system begins with an architectural constraint: the necessary four spandrels and their tapering triangular form. . . . Spandrels do not exist to house the evangelists. (pp. 339–340)

Robert Mark, the only participant in this debate with requisite architectural expertise, affirms our central point (while also noting the direct utility of pendentives in buttressing). He writes of our San Marco example (ref. 3, p. 386): “Domes mounted on arches create roughly triangular spaces in the corners, between the upper sides of the arches and the base of the dome.” For our second example, the diamond-shaped ceiling spandrels between the fan vaults in King’s College

Chapel, Mark both affirms the geometric necessity of the spaces and supports our claim (incorrectly challenged by Dennett in ref. 4) that the bosses hanging from the spandrels—the subsequent cooptation based upon symbols of Tudor power carved into the bosses and therefore the analog of the evangelists in the San Marco spandrels—represent a consequential use of a necessarily preexisting space and cannot be reasonably interpreted as the primary cause of the unified ceiling design. Mark (3) wrote:

The adoption of radially ribbed vaulting from a central plan to a square- or rectangular-planned bay leaves an opening created by the perimeter of the conoid tops that requires closure. . . . This is most simply effected by the placement over the opening of a large, flat stone plate [the spandrel in our usage]. The boss is actually only the ornament protruding from that plate. . . . Rather than providing an appropriate “ceiling to carry the Tudor symbols” [Mark here quotes Dennett’s claim that fan vaulting may have been chosen to yield spandrels for bearing the bosses, that could carry the Tudor symbols] it is far more likely that fan vaulting was selected for the college hall to adopt an up-to-date high architectural style. (p. 388)

Thus, spandrels are spandrels—that is, automatic byproducts 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.

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 is the primary structural decision and which the nonadaptive byproduct coopted for utility? Did the architects decide to mount a dome on arches, thus engendering the spandrels as a necessary consequence, or had the designers devised such a good plan for decorating spandrels that they persued the

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 “male-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 as 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 ornamented in a wide variety of ways, 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 Holofernes), 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 consequentially, 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 sequelae 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

area of the dome itself—so the two major substrates available for mosaic design are both substantial.

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 quadripartite 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. 1, 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 divided into quadrants, even though the dome itself 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, determine the fundamental design of a totality that ordained its consequential origin. The natural world abounds in recursions and feedbacks of this sort. Mustn't the ever cascading spandrels of the human brain be more weighty than the putative primary adaptations of ancient African hunter-gatherer ancestors in setting the outlines of what we now call "human nature"?

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 cooptation "for a widely different purpose" because the exapted 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 vertebrae 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 expressed as nonadaptive spandrels in 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 spread sheet, 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.

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