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PERSPECTIVE

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Spandrels and trait delimitation: No such thing as "architectural constraint"

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Forty years ago, Gould and Lewontin used the metaphor of a building's "spandrels" to highlight that organismal traits could be the inevitable consequence of organismal construction, with no alternative configurations possible. Because adaptation by natural selection requires variation, regarding a trait incapable of variation as an adaptation could be a serious error. Gould and Lewontin's exhortation spurred biologists' efforts to investigate biases and limitations in development in their studies of adaptation, a major methodological advance. But in terms of the metaphor itself, over the past 40 years there are virtually no examples of "spandrels" in the primary literature. Moreover, multiple serious confusions in the metaphor have been identified and clarified, for example, that the "spandrels" of San Marco are pendentives, and pendentives are perfect examples of adaptation. I look back over the sparse empirical fruits of the "spandrels" metaphor, and ask what the clarifications of the past 40 years mean for biological theory and practice. I conclude that if there is anything to be rescued from the clarified spandrels metaphor, it is not "constraint" at all. Instead, it is the still-unresolved issue of trait delimitation, which is how to parse organisms into subsets that are tractable and biologically appropriate for study.

1 | INTRODUCTION

The study of organismal form is often characterized as involving a dichotomy between internalist and externalist perspectives (Alberch, 1989; Sansom, 2009); in the 40 years since the publication of Gould and Lewontin's famous 1979 "Spandrels" essay, evolutionary biologists are increasingly overcoming this dichotomy (Badyaev, 2011; Olson, 2019). One half of the dichotomy is the "externalist" view, that is, that the field of morphologies that organisms can produce developmentally is so wide that it can be assumed that any restricted pattern of trait distribution is caused by selective agents in the environment. Passive and endlessly malleable organisms are molded for all practical purposes by selective forces external to developing individuals, hence, the term "externalism." The other half of the dichotomy is the "internalist" view, the claim that interactions between parts in developmental systems so bias the morphologies that can be produced that these factors are the decisive ones molding organismal trait distributions. Because it emphasizes processes occurring within developmental systems, and thus "internal" to developing individuals, it receives the designation "internalism." Gould and Lewontin's critique highlighted that an exclusively externalist view would necessarily overlook the crucial role of developmental processes in shaping the space of possibilities that can be exposed to selection. In doing so, they made reference to notions of evolutionary "constraint." Though "constraint" played a central role in their argument, they never defined this key term (Dennett, 1995). Their manifesto was likewise vague on the details of how to include "constraint" into the study of organismal traits, but their message was received by biologists, who set about incorporating development explicitly into studies of adaptation.

The result, the developmental approach to adaptation, is dissolving the internalist–externalist dichotomy (Olson,

MO designed the research and wrote the paper.

2019). The approach consists of explicit examination of whether apparently empty phenotypic space can be occupied or not (Badyaev, 2011; Olson, 2012). Finding that it can be occupied but that the occupants of those areas are of lower fitness than the commonly observed variants is consistent with traditional adaptationist accounts. Instead, finding that empty space variants are developmentally impossible or very difficult to produce is only a first step. Ulterior steps can create otherwise impossible variants via surgical or other manipulations. Finding that these creations have higher performance than the common variants is consistent with the notion that some sort of "constraint" exists, understood as a bias or lacuna in developmental space that is arbitrary with respect to function. In turn, this finding ushers in studies of the developmental dynamics that lead to the bias. Inevitably this research process uncovers footprints of both selection and "constraint." Because both "constraint" (however defined) and adaptation are involved in the production of any specific organismal trait distribution, once the details are in hand of the biological process shaping this distribution, declaring the trait to be shaped exclusively or even principally by internal or external forces adds no additional insight (Olson, 2019). In this way, Gould and Lewontin's highlighting of the internalist–externalist debate has helped overcome the dichotomy itself.

Part of the process of alloying the internalist and externalist views has involved careful reflection on the meaning of the term "constraint" (Antonovics & van Tienderen, 1991; Fitch, 2012; Maynard Smith et al., 1985; Olson, 2012; Pearce, 2011; Pigliucci & Kaplan, 2006; Sansom, 2009). The term continues to be refined, with phylogenetic, developmental, genetic, and even selective constraints being commonly used and debated in the evolutionary literature. Much remains to be addressed with respect to constraint, for example, whether the vague blanket term is even useful in building evolutionary theory or whether it is simply invitation for scientists to talk past one another (Antonovics & van Tienderen, 1991; Olson, 2012, 2019). As part of this effort, I use the 40 year "Spandrels" milestone to examine just one type of constraint, the centerpiece of Gould and Lewontin's essay, architectural constraint. To do so, I first examine the "spandrel" metaphor.

1.1 | The "spandrel" metaphor

"Spandrel" is one of the most transcendent metaphors of evolutionary biology (Pigliucci & Kaplan, 2006). Proposed in 1979 by Gould and Lewontin, the metaphor evokes the four massive triangles that on vast piers subtend the central dome of Venice's Basilica of San Marco. These triangles are lavishly decorated with mosaics, and the argument goes that they are so appropriate to the artist's composition that a viewer might easily think that the triangles were deliberately placed for creating harmony (Fodor & Piattelli-Palmarini, 2011; Havliček, Cobey, Barrett, Klapilová, & Roberts, 2015; Houston, 2009). The message of the spandrels metaphor is that the four triangles were not, despite all appearances, placed for bearing decorations, but are instead an example of "architectural constraint," the inevitable consequence of making a round dome fit onto a square base (Brigandt, 2015; Fitch, 2012; Raff, 2012). Gould and Lewontin challenged biologists to consider what this metaphor meant for studies of organismal form and function.

The metaphor galvanized evolutionary biology, and far transcended the field. In the years following Gould & Lewontin (1979), biologists were increasingly diligent about finding ways to make their studies of adaptation more rigorous, and to consider non-adaptive hypotheses more explicitly (Jaksić, 1981; Ketterson & Nolan, 1999; Larson & Losos, 1996; Losos, 2011; Olson, 2012; Pigliucci & Kaplan, 2006; Rose & Lauder, 1996; Sinervo & Licht, 1991). The metaphor has been particularly invoked in discussions of human psychological phenomena. Language (Botha, 2000; Fodor & Piattelli-Palmarini, 2011; Pinker & Bloom, 1990), music and dance (Dunbar, 2012), self-deception (Van Leeuwen, 2007), religion (Atran, 2004; Wilson, 2010), and aspects of human sexuality (Havliček et al., 2015; Lloyd, 2005) have all been examined from the point of view of the metaphor (see also the extensive list of Houston, 2009). Beyond biology, the spandrel metaphor is a fixture of the philosophy of biology (Fodor & Piattelli-Palmarini, 2011; Resnik, 1989) and is regarded as an archetype for construction of scientific arguments (Selzer, 1993) or rhetoric in general (Keith, 1997). Even the political implications of the metaphor have been debated (Prindle, 2009). This wide acceptance shows that the spandrels metaphor is firmly a part of thinking in evolutionary biology and beyond.

Despite this apparent solidity, over the past 40 years, biologists, philosophers, and architects have identified confusing aspects of the metaphor and offered important clarifications (Dennett, 1995; Houston, 1997; Mark, 1996; Park, 2007; Pigliucci & Kaplan, 2000; Rose & Lauder, 1996). The implications of these clarifications have been explored mostly in the philosophical literature (Dennett, 1995; Houston, 2009). The step that has not occurred, however, is for biologists themselves to return to the spirit of the metaphor, crucial clarifications in hand, to discuss what these insights might mean for biology (with the notable exception of Houston, 1997). In this essay, I review the metaphor and its clarifications. I then take the critical step of reevaluating the notion of biological "spandrels" in the light of these clarifications, asking what they mean for biological theory and practice. If the clarifications of previous authors are taken seriously, they lead to the conclusion that there is no such thing as architectural constraint as argued by Gould and Lewontin (Dennett, 1995). Instead, if there is anything to be

rescued from the clarified spandrels metaphor, it is the still-unresolved issue of trait delimitation, which is how to parse organisms into subsets that are tractable and appropriate for study. Before turning to the clarifications, it is necessary to ask what the metaphor was aiming to achieve.

1.2 | The spirit of the "spandrels" metaphor

"Constraints" in general can significantly affect explanations of trait variation that invoke adaptation, and Gould and Lewontin insisted that "architectural constraint" was one such type of constraint. In the sense they intended, architectural constraint denotes an inevitable consequence of the way something is constructed, with no other alternative constructions possible (Dennett, 1995; Gould & Lewontin, 1979; Grantham, 2004; Rosenberg & McShea, 2008). But adaptations represent a favored subset of a wider field of developmentally possible variants (Olson, 2012). The common variants are common because they are favored by selection. Gould and Lewontin intended "constraint" to refer to a situation in which the common variants are the only developmental possibilities. Because no other configurations are possible, then it could be incorrect to argue that these features are the favored ones from among a wider field of developmentally possible contenders. It could be that selection has extinguished all variation, leading to a lack of potential for response to selection. It could also be that features of development make the production of alternatives, even ones that would have higher fitness than the common type, impossible or nearly so (Fusco, 2001; Minelli, 2009; Olson, 2012). Any of these cases would drastically alter a typical selectionist account that explains trait distributions by appeal to ongoing selection on a wide pool of heritable developmental contenders (Raff, 2012). Because their architectural metaphor is not a very good one, it takes some effort to separate the spirit of Gould and Lewontin's argument from its content. Before arguing that the value for biologists in the spandrels metaphor is not what it says about "constraint," it is first necessary to review the important clarifications of the metaphor that have been made since 1979.

1.3 | The difference between spandrels and exaptations

"Spandrel" is frequently used in evolutionary biology as a synonym of exaptation, but the terms have distinct meanings (Fitch, 2012; Houston, 2009). As used by Gould and Lewontin, a spandrel is an "architectural constraint," a trait that is the inevitable consequence of organismal construction (Dennett, 1995; Gould, 1997; Houston, 2009). An exaptation (Gould & Vrba, 1982) is an organismal trait currently favored by natural selection that arose in a selective context different from the current one. Feathers may have first arisen in the context of thermoregulation and were then coopted (exapted) in the evolution of flight. In penguins, they were then exapted in the evolution of swimming. The "spandrels" holding up a church dome, supposedly there as inevitable "architectural constraints," are often coopted for decorations. Both spandrel and exaptation as biological terms have been criticized. All organismal parts include some preexisting elements (Dennett, 1995; Griffiths, 1992), so most traits can be considered exaptations, and, as explained below, the architectural metaphor is a bad one. But whatever the limitations of the terms, again, their spirit is well taken: function does not indicate origin, and, as used by Gould and Lewontin, a "spandrel" can be an exaptation, but an exaptation is not necessarily a spandrel (Houston, 2009; Pievani, 2013). While the spandrel/exaptation distinction does cause confusion, it pales in comparison to that caused by the spandrel/pendentive distinction.

1.4 | Gould and Lewontin's "spandrels" are pendentives, and pendentives are perfect examples of adaptation

In their efforts to implement the spirit of the "spandrels" critique, biologists and others set about examining the metaphor closely, only to find that, rather than "constraint," it is a perfect example of selection in action (Dennett, 1995; Houston, 1997; Pigliucci & Kaplan, 2006). Metaphors in biology are supremely useful tools, helping direct research into novel directions (Falkner, 2016). One of the ways metaphors do this is by highlighting otherwise unseen analogies in biological systems. For example, the adaptive "radiation" metaphor evokes energy streaming in all directions from a central point. This evocation directs countless research efforts to understand the rapid divergence of species from a single common ancestor into multiple metaphorical directions in functional space (Olson & Arroyo-Santos, 2009). Squeezing the maximum potential out of a metaphor requires careful reflection on the metaphor's analogical implications. In the effort to study "architectural constraint," turning to the details of the "spandrels" metaphor was natural.

On examination, Gould and Lewontin's "spandrels" turned out to be structures called "pendentives," and an excellent example of selection in action. Gould and Lewontin's "architectural constraint" designated an inevitable constructional consequence, with no other alternative constructions possible (Grantham, 2004; Rosenberg & McShea, 2008). The triangular wedges holding up the Basilica's dome are huge masses of masonry known as pendentives. Far from being inevitable, pendentives have their own shape and size that could easily vary independently of the dome (Dennett, 1995; Houston, 2009; Olson, 2012). This variation, moreover, would have performance consequences. Mark (1996) has

detailed the variation observed worldwide in the ways that domes are supported. It turns out that there are lots of ways that domes are supported in real buildings, and there is an infinite number of ways that domes could be supported in imaginary buildings (Olson, 2012). By the same token, there would seem to be an infinite number of ways to build a pendentive—they could be made very small, or stretch to the ground, or be huge and blocky (Dennett, 1995), so, far from "constrained," the space of possibilities for dome supports is very wide.

Although dome supports can imaginably vary widely in shape and size, it turns out that very few variants are effective in supporting the weight of a large dome. The one that works best, that is, keeps the dome from falling down for the longest period with the least material, turns out to be pendentives (Dennett, 1995; Houston, 1997, 2009; Mark, 1996). So pendentives are the variant from among a very wide field of possibilities with the highest architectural "fitness." The persistence of the fittest of the possible variants is simply selection, and has nothing to do with constraint, making the "spandrels" example one of selection in constraint's clothing, that is, using vague constraint terminology to refer to selection. Therefore, to extract the insight Gould and Lewontin intended, for the rest of this essay, I will no longer take "spandrel" to refer to pendentives or exaptation. Instead, we need to turn to real spandrels, which really are inevitable architectural byproducts (Mark, 1996).

1.5 | Pendentives are "things"; Real spandrels aren't

In contrast to a pendentive, a spandrel really is "a predictable form that arises as a side consequence" (Gould 1997, p. 10751), and this is the sense that Gould and Lewontin intented for "architectural constraint" (Mark, 1996). As a result, it is in this, non-adaptive, sense of the metaphor that biologists should search for evolutionary analogies. As used in architecture, a "spandrel" is a space left over between architectural elements (Cowan, Smith, & Chow, 2004). The shape and size of a spandrel is determined not by its own characteristics but by virtue of the surrounding elements. The usual use of the term is to denote the triangular spaces between arches. As the arches vary in size and shape, so do the spandrels (Figure 1). The spandrels cannot vary

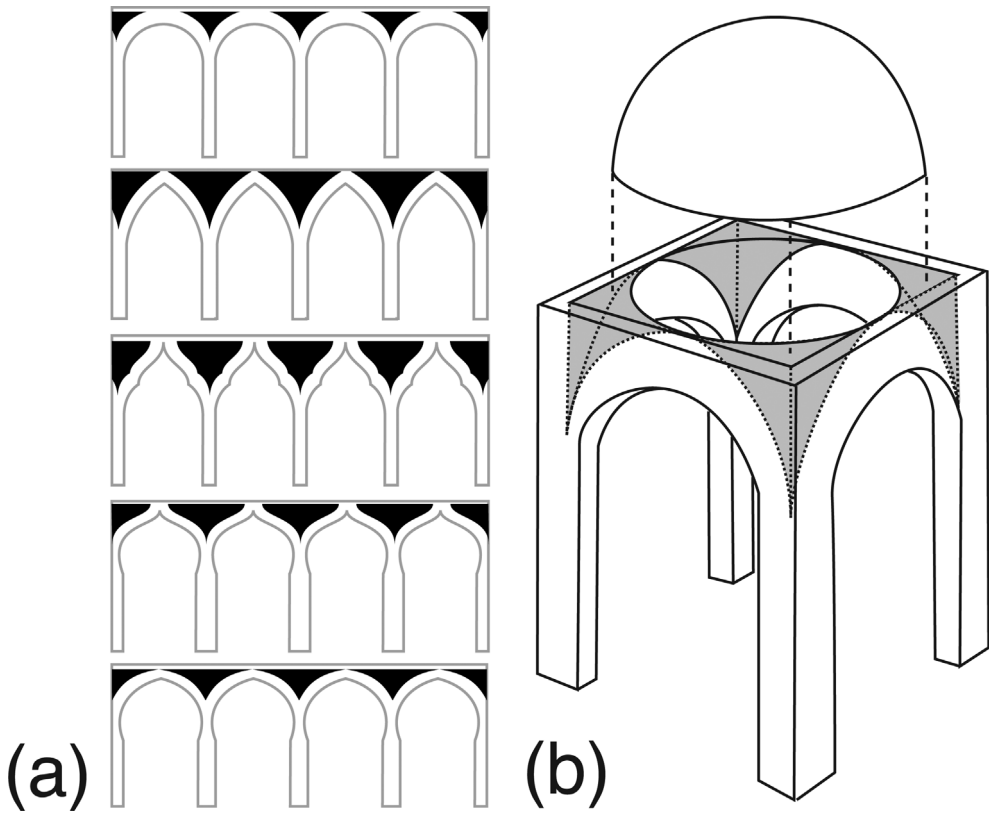

FIGURE 1 Spandrels as "not-things," pendentives as "things." (a) Spandrels (black) are simply the leftover space between arches. Although wall material in this area can serve mechanical support or decorative functions, the exact size and shape of the space between the arches is determined by the size, shape, and spacing of the arches, not the inherent characteristics of the spandrels themselves. (b) In contrast, pendentives (gray) are "things" that can vary to an extent independently of the surrounding arches and dome. These great masses of masonry can be large, small, variously shaped, and made of virtually any material, but only configurations similar to the one depicted work well for holding up a large dome with a minimum of material

independently of the arches because they are the spaces between the arches. Another use of "spandrel" is the space below a staircase, which is eminently exaptable as storage, but again its size and shape are defined not by its independent characteristics but by the height and pitch of the staircase. True spandrels are not things but simply spaces left over between things. To see why "thingness" is important for adaptation, we must turn to the idea that organisms can be decomposed into "parts."

1.6 | Adaptation, biological "parts", and the importance of trait quasi-independence

Studies of adaptation focus on traits of organisms, for pragmatic reasons, but also, and more significantly, for biological ones. From a pragmatic point of view, it is clear that a biologist cannot measure every possible variable describing a system. So, for purely practical reasons, biologists often need to focus on parts rather than whole organisms. But notions of parthood in biology run far beyond practicalities. Biologists routinely speak of "parts" of organisms as adaptations, as in "the wing is an adaptation for flight" (Araya-Ajoy & Dingemanse, 2013; Lewontin, 2000). This talk goes hand in hand with talk of a part being "an" adaptation. This language invokes the idea that an organismal trait is an identifiable entity in nature (Assis & Brigandt, 2009; Larson & Losos, 1996; Lewontin, 2000; Rieppel, 2005; Vogt, 2018; Wagner, 1989). If "parts" can be adaptations, then the part must be able to respond to natural selection to an extent autonomously from the rest of the body (Araya-Ajoy & Dingemanse, 2013; Breuker, Debat, & Klingenberg, 2006). This partial evolutionary autonomy is what Lewontin termed quasi-independence (Lewontin, 1977, 2000; also Wagner, 1989, 2001).

Quasi-independence is manifest in the evolution of morphological diversity across species (Drake & Klingenberg, 2010; Eble, 2005; Frankino, Emlen, & Shingleton, 2010). The spurge family (Euphorbiaceae), for example, has perhaps the highest habit diversity of all plant groups, with cactus-like spherical members, medusa-head succulents, trees, shrubs, and herbs, all of which have a relatively invariant floral display (Figure 2a–c). If all parts of organisms were very tightly linked to one another, such relative independence between floral display and habit would be impossible. Phenomena such as heterochronic alteration of "parts" would be impossible, as would homoeosis, when a given "part" is produced in a different serially homologous region (Olson & Rosell, 2006; Raff & Raff, 2000). Heterotopy, such as the production of flowers on tree trunks or on leaves rather than the standard location from buds on twigs (Figures 2d and 2e) is another example that suggests that some parts are largely developmentally independent of others (Baum & Donoghue, 2002). It is this developmental quasi-independence that seems to justify the atomization of organisms in studies of adaptation (Lewontin, 2000).

Lewontin used the term "quasi-independence" because independence of parts cannot be complete. Organismal parts like ears, leaves, or organelles are always found as part of an organism, and cannot exist independently of one (Lewontin, 1977, 2000; Rieppel, 2005). Organsims function as integrated wholes. Birds and bats fly not just because they have wings but because of their bone structure, lung physiology, musculature, and metabolism. Yet studies of wing dimensions, without reference to the rest of the body, nevertheless seem to prove highly informative regarding variation in lifestyle across species (Farney & Fleharty, 1969; Kruyt, Quicazan-Rubio, van Heijst, Altshuler, & Lentink, 2014). So while it is clear that organisms are integrated wholes, some organismal sectors clearly develop, and therefore can evolve, to an extent independently of the rest of the organism, and this quasi-autonomy appears to cash out in the usefulness of part-speak in evolutionary biology (Araya-Ajoy & Dingemanse, 2013; Breuker et al., 2006; Wagner, 2001). To have the potential for sending an adaptationist explanation off the rails, a putative spandrel must present a very real risk of being regarded as a quasi-autonomous "part," because these are the organismal subsets that can potentially respond to natural selection quasi-independently of the rest of the organism.

1.7 | Spandrels are not "parts"

If mistaking spandrels for real parts is a latent risk to studies of adaptation, then the primary literature should be filled with examples. Remarkably, given the traction of the metaphor, virtually all of the examples to be found are simply misapplied synonyms for exaptation. Also remarkable is that, given that the central architectural metaphor would apply most straightforwardly to organismal morphology, none of the examples of morphological spandrels come from detailed empirical study in the primary literature (Table 1). Instead, virtually all "architectural constraint" spandrels in the literature are found in the secondary literature and are offered as examples based on the author's intuition rather than research. What all spandrels *qua* architectural constraint have in common is that none of them represent "traits" or "parts" that could respond quasi-independently to selection. This implies that practically no biologists have had their adaptationist research programs sent astray, seduced by the apparent adaptive significance of a spandrel.

And when they have, the trait has inevitably been a human attribute. This is a crucial consideration because countless human traits are unique to our species, meaning that standard comparative methods, which require variation in a trait across multiple species, aren't available (Olson & Arroyo-Santos, 2015). Many other tools of adaptationist evolutionary biology are also unavailable for studies in humans, such as selective

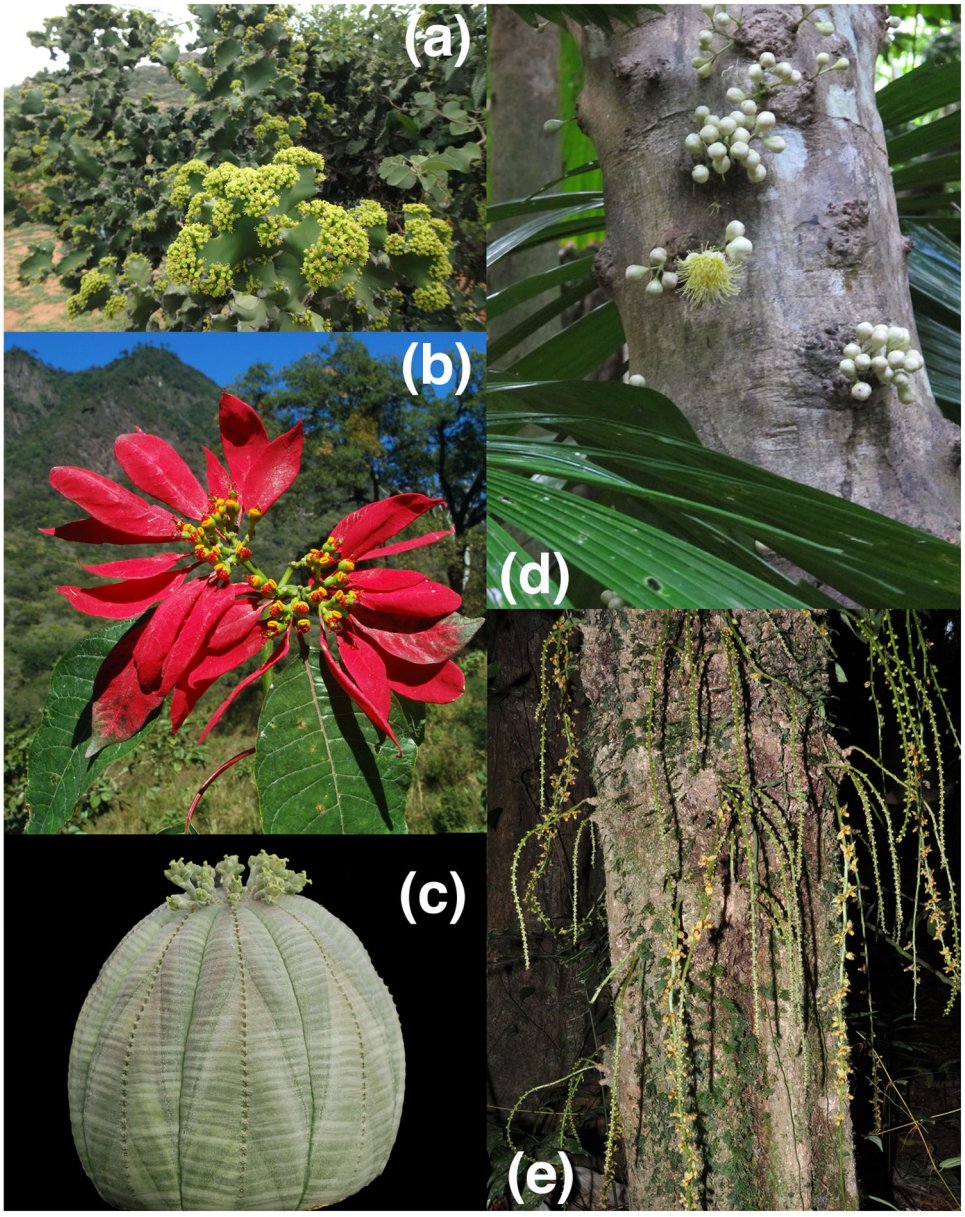

FIGURE 2 Evidence for trait quasi-independence in the evolution of morphological diversity. (a–c) The plant genus *Euphorbia* spans a very wide range of vegetative morphologies, but their flowers are all clustered in similar structures called cyathia. Plants can range from (a) giant tree succulents like the Indian *Euphorbia antiquorum*, (b) small trees such as the Christmas poinsettia of Mexico (*Euphorbia pulcherrima*), or (c) South Africa's tiny spherical-bodied *Euphorbia obesa*. Across all of this variation, the structure of the cyathia varies little. (c and d) Most trees bear flowers on twigs, but some bear them on their trunks, a phenomenon known as cauliflory, as in (d) *Syzygium cormiflorum* or (e) *Ryparosa javanica*, both of northeast Australian tropical rainforests. Neither the variation of *Euphorbia* life form diversity relative to cyathial morphology nor cauliflory as compared to the usual twig-borne flowers would be possible if some organismal subunits were not developmentally quasi-independent of others. Discovering the limits of these subunits and the causes of these limits is a major research effort within evolutionary biology

breeding, directed mutagenensis, or surgical alteration to create variation, so it is often hard to amass much of the key evidence that evolutionary biologists use to distinguish between alternative explanations in non-human systems (Olson, 2012; Olson & Arroyo-Santos, 2015; Pavličev & Wagner, 2016). It is thus understandable that competing alternative explanations for the presence of human traits should generate persistent debate (Forber, 2009). This is especially the case for behavioral and psychological traits, where the very notion of "trait" is even farther from clarity than it is in morphology (Araya-Ajoy & Dingemanse, 2013; Park, 2007; Wainwright & Friel, 2001). Examples of morphological spandrels from the literature are summarized in Table 1, with two examples sufficing in what follows to illustrate that spandrels are not traits that can respond to selection quasi-independently of the rest of the body.

TABLE 1 Examples of morphological "spandrels" from the literature, showing that they are productively viewed as problems of trait delimitation

Proposed spandrel	Why an issue of trait delimitation	References
Human chin	Selection favoring faster receding of the dentary with respect to the mandibular bone leaves a projection called the "chin." Understanding evolution of the "chin" requires identifying to what degree it can vary heritably and the relevant quasi-independent developmental units.	Depew and Weber (1997), Lewontin (2000)
Female orgasm	Selection favors dependable male orgasm; women inherit an excitable organ and response because of shared developmental pathway. Much evidence favors the notion that the female orgasm should be studied as non-independent of selection on the male orgasm, and that the developmental unit under selection remains to be characterized in detail.	Lloyd (2005, 2013) (see also Pavličev & Wagner, 2016; Wagner & Pavličev 2017)
Fontanel	Assuming that selection favors delayed cranial closure, then understanding why requires identifying the quasi-independent developmental fields in the bones involved.	Held (2009)
Gastropod umbilicus	Assuming that selection favors umbilicus presence, then understanding why requires identifying the quasi-independent developmental fields in the surrounding shell.	Gould (2002)
Male nipples	Selection favors functional nipples in females; males have them because of shared developmental pathways. Understanding the presence of this trait would seem to require that the developmental unit under selection needs to be characterized in detail.	Held (2009)
Sympathetic changes in serial homologues	Serial homologues often show a lack of developmental independence because of shared developmental mechanisms. It is essential to document the degree to which serial homologues can or cannot diverge under selection (in some cases, they can diverge very markedly, as in the middle figer of the aye-aye Daubentonia).	Held (2009)
White bones	Selection favors calcium in bones irrespective of color. The whiteness of bones is not a feature that varies independently of calcium content (or even one that has been proposed as being under selection).	Park (2007)

1.8 | Paragon spandrels are non-parts: The gastropod umbilicus and the female orgasm

A much-cited example of a morphological "spandrel" is the gastropod umbilicus, a case that illustrates that "architectural constraint" cannot possibly refer to a trait with the requisite quasi-independence to be considered a potential adaptation. The umbilicus (Gould, 2002; Kuźnik-Kowalska, Proćków, Pląskowska, & Pokryszko, 2007) is an important example because it is often accepted as a perfect example of a spandrel, one so solid that it can guide the search for other spandrels by following its analogy (Botha, 2000). The umbilicus is a hollow space along the central axis of some snails (Figure 3). In some species, the space is used for carrying eggs, sometimes consistently, sometimes only occasionally (Kuźnik-Kowalska et al., 2007). This is a fine example of exaptation, but mistaking the umbilicus for an adaptation would require interpreting the umbilicus as quasi-independent of the rest of the snail shell. Otherwise, there would be no sense in considering it a possible adaptation, that is, a trait that can respond to selection to some extent independently of the rest of the body. In the case of the umbilicus, this is a clear impossibility.

Just like the spaces between arches and spandrels, the space between the gyres of a snail shell is constitutive of the umbilicus, not quasi-independent of the shell. Flagging the umbilicus as an example of "architectural constraint," understood as a lack of developmental alternatives, would require contrasting this constraint scenario with an adaptationist one. The adaptationist scenario would necessarily assume ancestral populations in which the umbilicus varied quasi-independently of shell coiling parameters and shell wall thickness. It requires assuming that, of this wide field of variants, certain variants were favored over others. Because the shell coiling parameters and shell wall thickness characteristics are constitutive of and not quasi-independent of the umbilicus, it is impossible that a biologist would be tempted by such a scenario. In fact, even though the umbilicus is presented as a paragon of spandrelhood (Botha, 2000; Gould, 2002), no biologist has ever been tempted to study the umbilicus as (quasi-) independent of the rest of the shell. The following example, though, illustrates a case in which biologists do appear to have misidentified a "spandrel" for a trait under current selection.

The best-documented case of a "spandrel" sending adaptationist studies awry is the the human female orgasm.

FIGURE 3 The gastropod umbilicus. The hollow space, known as the umbilicus, in the coils of some snails, as in this *Polygyra* from tropical Mexico, is often mentioned as representing a biological "spandrel." A "spandrel" is understood as a "leftover" empty space amid real architectural elements. The umbilicus has been coopted in some snail species as a brood chamber, but this does not mean that it is a "part," a trait than can respond quasi-independently from the rest of the shell to selection. This is because the umbilicus is simply a leftover space between real parts, not a part itself, again emphasizing the importance of trait delimitation in studies of adaptation

Various hypotheses have been proposed to account for the current adaptive value of orgasm in women, ranging from its ability to increase pair bonding and therefore parental care, to increasing sperm retention or stimulating ovulation (Gould, 1987; Komisaruk, 2016; Lloyd, 2005, 2013; Pavličev & Wagner, 2016; Wagner & Pavličev, 2017). All of these hypotheses generate clear predictions regarding features such as the dependability of orgasm per copulation event, the placement of the clitoris relative to the vagina, and numerous physiological responses. In all cases, support for the predictions seems weak. An alternative account, though, is consistent with all the data. It is that potent selection favors the dependability of male orgasm. Males and females share much of their early morphological development, and as a result the precursor of the penis, with its dense nerve supply and excitability, is present in both male and female embryos. Any males in which orgasm were not dependably associated with intercourse would have low mating success and thus selection favors dependable male response (see also Pavličev & Wagner, 2016; Wagner & Pavličev, 2017). No adaptive hypothesis positing current utility is able to explain why, in contrast, female orgasm is not as dependably associated with fitness. However, if the female response is the result of selection favoring the male response, then this variability, which has no dependable association with fitness, would be expected. It is not clear why males and females share so much of their early morphological development, and indeed this would seem the outstanding empirical question. Because the shared developmental pathway between males and females is an issue for empirical investigation, and is not clearly an "inevitable byproduct of organismal construction," then this prime example of a "spandrel" does not exemplify any sort of "architectural constraint" but rather biologists mistakenly regarding the female orgasm as a trait independent of that of the male. From this point of view, the most important challenge with regard to the female orgasm is to individuate the evolutionary "character" that it represents a variant of (Pavličev & Wagner, 2016; Wagner & Pavličev, 2017).

There is no need for "constraint" language in these situations, simply careful identification of the developmental unit under selection. Designating situations such as the umbilicus or the female orgasm "architectural constraint," or indeed "constraint" of any kind, does not provide any empirical direction or theoretical clarity. Instead, they exemplify, as do all clear examples of "spandrels," an issue that Lewontin championed even before the spandrels paper, one he called "arbitrary atomization" in studies of adaptation.

1.9 | The persistent problem of trait delimitation

Lewontin (1977, 2000) contrasted "arbitrary atomization" with appropriate delimitation of organismal subsets for studies of adaptation. The limits of a "part" studied as an adaptation should align as closely as possible with real quasi-independent biological units. This alignment increases the probability that data will reflect selection and other factors shaping organismal form (Breuker et al., 2006; Montes-Cartas et al., 2017; Wagner, 1996). To the extent that the limits of "parts" studied are arbitrary, then the likelihood that the data will reflect spurious patterns would seem destined to increase (Mitteroecker, 2009). A major step in adaptationist studies is therefore trait delimitation (Larson & Losos, 1996).

A battery of statistically sophisticated quantitative approaches are available for studying trait independence and lack thereof, but methodological profusion and complexity are not the same thing as theoretical clarity. There are countless approaches for delimiting organismal subsets, based on morphological data from traditional linear measurements to geometric morphometrics (Goswami & Polly, 2010a; Magwene, 2001). Much of quantitative genetics is directed at identifying patterns of dependence and independence between traits, and many other techniques are deployed under the rubrics of modularity and phenotypic integration

(Cheverud, 1995; Esteve-Altava, 2017; Melo, Porto, Cheverud, & Marroig, 2016). Across the individuals of a given species, it is certainly possible to collect data on the associations between organismal parts and thereby identify statistically independent subsets (Magwene, 2001). However, when the statistical thresholds are varied or different statistical approaches used, then the resulting inference of how many "parts" or modules are present varies accordingly (Goswami & Polly, 2010a; Montes-Cartas et al., 2017; Perez, de Aguiar, Guimarães, & dos Reis, 2009). For instance, different authors have reported different modular skull structures in mammals. Drake & Klingenberg (2010) recovered a two module model, Cheverud (1995) a six module model and Goswami and Polly (2010a) a different six module model (see Table 1 in Goswami & Polly 2010a) for the same biological structure. The profusion of methods, however, gives no directive showing which set of modules is the most evolutionarily relevant (cf. Pearce, 2011 on what counts as a "variant").

The most promising strategy to identify evolutionarily relevant modules appears to be to combine intraspecific delimitations of modules with interspecific ones, in the form of comparative analysis of lineages that have diversified in such a way that evolutionarily quasi-independent subunits can be identified (Eble, 2005). Analyses including comparative, not just contemporary intraspecific ontogenetic or quantitative genetic data, are advantageous because they can describe situations in which the quasi-independence was enough to allow for the evolution of interspecific diversity, and which intraspecific module delimitations coincide with those actually observed in across-species diversity (Adams & Collyer, 2009; Beltrao, Cagney, & Krogan, 2010; Drake & Klingenberg, 2010; Goswami, 2006; Goswami & Polly, 2010b; Hunt, 2007; Parsons, Márquez, & Albertson, 2012). Studies of geometric morphometrics and quantitative genetics within and across species are currently the bedrock methods in this regard (Beldade, Koops, & Brakefield, 2002; Beltrao et al., 2010; Drake & Klingenberg, 2010; Goswami & Polly, 2010b; Parsons et al., 2012; Porto, de Oliveira, Shirai, De Conto, & Marroig, 2009). Also, studies of heterochrony, homeosis, or heterotopy help show which "parts" can change independently of others, or which can be produced more or less without alteration in novel contexts (Olson & Rosell, 2006; Raff & Wray, 1989; Schmidt & Starck, 2010). The analyses of phylogenetic systematics are predicated on the notion that characters must be independent of one another, and often uncover patterns of correlated or uncorrelated change across species. This is why the first step in Larson and Losos's (1996) methodology for studying adaptation begins with the assessment of taxic homology, because these traits are putatively independent of one another. Biologists are far from consensus, though, and some reasoning suggests that including comparative data might not in fact resolve methodological ambiguity, and even that notions of modularity might not coincide with biological reality (Mitteroecker, 2009).

That there is at present no clear means of delimiting organismal traits with confidence is why the debate over just what a character, trait, part, or even variant is in evolutionary biology is an ongoing one (Araya-Ajoy & Dingemanse, 2013; Esteve-Altava, 2017; Pearce, 2011; Vogt, 2018; Wagner, 1996, 2001). Nature often provides little directive regarding how organismal "parts" should be delimited as different entities, in the natural way, for example, that chimpanzees and humans seem clearly different entities. This is perhaps one reason that the issue of trait delimitation was eclipsed in the "Spandrels" paper, though it was mentioned there, in favor of flashier-sounding but confused notions of "constraint." What is clear is that there is still much to understand regarding what biologists mean when they speak of "parts" or "traits" (Mitteroecker, 2009). But because the notion of "parts" is central to evolutionary biology, this issue is one that requires clarity and attention as much today as it did 40 years ago.

1.10 | Replacing the metaphor

A good metaphor spins off countless research topics, but "spandrels" is not one of these. For more than a century, biologists have been inspired by the "adaptive radiation" metaphor, with no end in sight for the metaphor's utility. The "spandrels" metaphor has not been so fertile. Given the prominence of the metaphor, if it were a biologically meaningful and scientifically productive one, then there should be abundant examples of spandrels in the literature. To be sure, Gould and Lewontin did help inspire biologists to include exploration of developmental bias and potential in their adaptationist studies (Olson, 2012). Yet virtually no examples of spandrels are found driving research in the primary literature. Those that are seem clear misapplications of the metaphor, usually as a synonym of exaptation. Instead, what all of these examples illustrate is that spandrels are not "parts" (Table 1). For a biologist to send research truly awry, he or she would need to mistake a non-independent trait for a quasi-independent one, and while it surely happens, this is something that biologists earnestly take pains to avoid. It is also a problem that admits of continual course-correction, as research on trait quasi-independence, modularity, and phenotypic integration show. And even the cases in which scientific research has focused on a non-independent trait, as in the case of the female orgasm (Table 1; Lloyd 2005; Pavličev & Wagner 2016), nothing in the idea of "architectural constraint" has offered any empirical direction or theoretical insight. Instead, asking whether a given trait could be delimited in a way that is more appropriate to the question at hand points the way to illuminating investigation. As a result, the usefulness the "spandrels" metaphor holds for biologists is not found in notions of "constraint," architectural or otherwise. Instead, the

spandrels metaphor highlights the problem of trait delimitation and the importance of identifying evolutionarily relevant developmentally quasi-autonomous organismal subsets (the perspectives of Park, 2007; Lewens, 2009 regarding "spandrels" seem compatible with this conclusion).

The meaning of the term "spandrel" can thus be adjusted, from "a trait that is an inevitable consequence of organismal construction and for which variation is unlikely or impossible" to "an incorrectly delimited trait, one made up of arbitrary subsets of two or more quasi-independent organismal subunits." This clarification has important advantages. It obligatorily distances biological thinking from "constraint" vocabulary, which is dangerously vague and can always be replaced by more precise language (Olson, 2012, 2019). Instead, identifying a problem of trait delimitation gives welcome guidance, pointing to the need to explore the limits and causes of organismal subsets (Araya-Ajoy & Dingemanse, 2013). Along these lines, the most important challenge in trait delimitation is for theory, that is, the biological reasons to delimit modules or "parts" in one way and not others, to catch up to the sophistication of the many methods available. In this way, the clarifications to the "spandrels" metaphor of the last 40 years highlight the very real and truly challenging problem of trait delimitation as a central research effort of its own.

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CONFLICTS OF INTEREST

There is no conflict of interest to declare.

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