

**Innovation in Cultural Systems**  
**Contributions from Evolutionary Anthropology**

**edited by Michael J. O'Brien and Stephen J. Shennan**

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# 1 Issues in Anthropological Studies of Innovation

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It would be difficult to find a topic in anthropology that has played as central a role as innovation in attempts to explain why and how human behavior changes. Likewise, it would be difficult to find a topic that has caused more debate and resulted in such a lack of consensus. At first glance, this might seem a little odd, given that the term *innovation* is used so widely and has what appears to be a straightforward definition: something new and different. Although there is nothing wrong with that definition, it barely scratches the surface of what in anthropology has turned out to be a complicated concept. For example, the definition doesn't tell us how we would recognize an innovation, nor does it tell us anything about its origin.

Of course, a simple definition shouldn't be held to such a high standard, but it might be helpful if those using the term for more than casual purposes were specific about such matters. Such has rarely been the case in anthropology, although it hasn't been for lack of trying. Anthropologists for over a century have recognized the complexity of the conceptual and methodological issues surrounding innovation, especially with respect to units and scale. In short, how do we identify not only innovations but the units involved in the transmission of those innovations? Are they the same units that we can use to measure transmission? Are there different scales of units, with units at one scale subsuming those below them?

Here we briefly examine those issues, bypassing extended discussion of any single topic and focusing instead on the development of some of our current notions of innovation. Definitions of this term and its relation to "invention" have varied considerably. Fagerberg (2005), for example, regards invention as the first appearance of an idea for a new product or process, whereas innovation represents the first attempt to put it into practice, which may occur considerably later. Moreover, innovation may be seen not as a "one-off" but as a continuing accumulation of changes (see chapter 9, this volume). Barnett (1953: 7–8), on the other hand, claims to be following popular usage in regarding inventions as physical things, whereas an innovation is defined as "any thought, behavior or thing that is new because it is qualitatively different from existing forms," which sets the bar quite high

with its emphasis on the qualitatively novel. The distinction made by Elster (1986) in his study of technical change corresponds closely to that advocated by Fagerberg, in that innovation is viewed as “new technical knowledge” (p. 93) and invention as the generation of a new idea. Elster also points out that diffusion often involves innovation, as modifications to a product or process are made in response to a new context, whereas substitution, making a change in some process using existing technical knowledge, also easily shades into innovation.

Schumpeter (1934) placed his main emphasis on the qualitative disjunction side— “[Innovation] is that kind of change arising within the system which so displaces its equilibrium point that the new one cannot be reached from the old one by infinitesimal steps. Add successively as many mail coaches as you please, you will never get a railway thereby” (Schumpeter 1934: 64). Schumpeter also gave a role to adaptive technical change and the importance of the accumulation of small changes over time (Elster 1986). Whether such innovations, small and incremental or large and discontinuous, will be successful is another matter again and depends on the various selection and bias processes discussed below.

Most discussions of innovation have focused on the technical dimension, including the organizational aspects of technical processes, as the discussion above suggests. However, there is no reason why fashions should not be included, and here success, in terms of increasing frequency, may be simply the result of the vagaries of random copying (see chapter 8, this volume). Indeed, as contributors to this volume make clear, the issue of innovations in cultural systems is almost unlimited in terms of scope, and we leave it to our colleagues to explore the myriad directions that lie beyond our focus.

Although it is sometimes forgotten, much of what we take for “modern” perspectives is actually built to varying degrees on decades of thoughtful research by our forebears. We were reminded of this recently while perusing the abundant social science literature on memes, which some social scientists argue underlie the spread of innovations. It would be worthwhile for those interested in memetics to spend an afternoon or two looking at how ethnologists and archaeologists of the first half of the twentieth century wrestled with what culture traits are. The parallels in thought processes, analytical approaches, and even research dead ends are enlightening.

### **Anthropological Views on Innovation**

Innovation was explicit in the nineteenth-century writings of ethnologists such as Tylor (1871) and Morgan (1877), both of whom viewed the production of novelties—new ideas, new ways of doing things, and the like—as the underlying evolutionary force that propels cultures up the ladder of cultural complexity. Innovation was equally important in the work of later cultural evolutionists such as Steward (1955) and White (1959). For them,

the evolutionary process was less orthogenetic than it was for the earlier evolutionists, with the source of innovation wrapped up in the kind of mechanisms a group needs to meet the challenges of its physical and social environment.

Innovation has also played an essential role in American archaeology (Lyman 2008; Lyman and O'Brien 2003; Lyman et al. 1997; O'Brien et al. 2005). Culture historians of the twentieth century routinely looked to diffusion and trade as sources of innovations, and hence of culture change, adopting without comment the models of their ethnological colleagues. Sometimes innovations were viewed as having been borrowed, often from incredible distances (e.g., Ford 1969; Meggers et al. 1965). Other times they were viewed as products of what Adolf Bastian referred to in the mid-nineteenth century as the "psychic unity of mankind" (Lowie 1937: 35). These two contrasting processes—diffusion versus independent invention—were at the heart of discussions of cultural relatedness. Thus, Steward (1955) argued that if the ethnologist (or archaeologist) could determine which traits were at the core of a culture and which ones were secondary, then the traits could be used to assess the degree of cultural relatedness between that culture and others. The more core traits that two cultures possess, the more historically related they are. If two cultures hold few or no traits in common, then either the cultures are unrelated or they were once related but at such a distant point in the past that the phylogenetic signal has all but disappeared.

### *Units of Culture in Twentieth-Century Anthropology*

Despite the widespread use of culture traits as measures of relatedness or of functional convergence, there was much less emphasis on trying to figure out exactly what a culture trait *is*. This raises particular difficulties if our focus is innovation because if we cannot even define the cultural features we are dealing with, deciding what represents an innovation is problematical in the extreme. Researchers universally assume that such traits are mental phenomena that one acquires through teaching and learning, but through much of the twentieth century there were few explicit theoretical definitions of a culture trait (Osgood 1951). This was highly problematic and meant that the units varied greatly in scale, generality, and inclusiveness (Lyman and O'Brien 2003). There were numerous efforts to resolve the difficulties of classification and scale (e.g., McKern 1939; Willey and Phillips 1958), but they did little to resolve the issue.

Biologists might well point out that there are also procedural problems in their discipline, where there is no standard set of characters used in the creation of taxa, but the situation is murkier in anthropology (see chapters 3 and 4, this volume). The one place where anthropologists *have* made insightful comments is with respect to what early in the twentieth century became known as *trait complexes*—minimally defined as "groups of culture elements that are empirically found in association with each other" (Golbeck 1980).

Although trait complexes have traditionally been used as another means of comparing cultures, the concept has a role to play in modern cultural evolutionary analysis, if for no

other reason than it reminds us that cultural phenomena may evolve as complex wholes, not as tiny parts (Boyd et al. 1997; Guglielmino et al. 1995; Henrich and McElreath 2003; Pocklington 2006; Shennan and Steele 1999; chapter 14, this volume). Selection can, and often does, act as a tinkerer—and “one who does not know exactly what he is going to produce but uses whatever he finds around him” (Jacob 1977: 1163)—but it is the potential “cascading” effects (Schiffer 2005; chapters 13 and 14, this volume) of that selection that may be important. A key goal of evolutionary analysis is to identify which applies in any given case, rather than making blanket assumptions about the holistic or atomistic nature of innovation and change.

Our point is that novelties are often more than simple character-state changes (Basalla 1988; Reid 2007). This is more or less what Trigger (1998: 364) apparently had in mind when he said that evolutionary archaeology should abandon a “reductionist biological terminology in favor of one that explicitly takes account of the unique, emergent aspects of human behavior.” Of course, the insistence on human uniqueness is overdone; biological evolution has plenty of examples of the emergence of entirely new phenomena (see, e.g., Maynard Smith and Szathmary 1995). Nevertheless, “emergent aspects”—aspects that have irreducible novel properties—are important considerations in any discussion of cultural innovation (O'Brien 2007; Sawyer 2005; Shennan 2002a). Recent evolutionary approaches to culture have had to address the “units of culture” issue head-on, and their contribution is outlined below.

### **Cultural Transmission—The Spread of Innovation**

From the beginning, regardless of how ethnologists and archaeologists viewed culture traits, and irrespective of their arguing over whether a particular trait was transmitted vertically (cultural ancestor to cultural descendant) or horizontally (cultural group to unrelated cultural group),<sup>1</sup> there was agreement that traits are learned, not genetically inherited (see chapter 3, this volume). Transmission, particularly between parents and offspring of the same sex (Shennan and Steele 1999), creates what archaeologists have long referred to as *traditions*—patterned ways of doing things that exist in identifiable form over extended periods of time (chapters 9, 10, 13, and 15, this volume).

It seems naive, given what we know of the archaeological record, not to believe that forms are modeled on preexisting forms. Further, cultural phenomena are parts of human phenotypes in the same way that skin and bones are, and as such they are capable of yielding data relevant to understanding both the process of evolution and the specific evolutionary histories of their possessors.

With the growing interest in evolution that became noticeable in anthropology in the 1960s and accelerated through the 1970s and 1980s (e.g., Campbell 1965, 1970, 1975; Dunnell 1980; Durham 1976, 1978, 1979, 1982; Rindos 1980), researchers began to

reconsider the relationship between biology and culture (see chapters 2 and 5, this volume), and nowhere was this more evident than in attempts to understand the role of innovation in the evolution of cultural systems. One area of sustained focus not only in anthropology but in the social sciences in general was *cultural transmission* (e.g., Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1973, 1981; Cloak 1975; Durham 1991; Lumsden and Wilson 1981; Pulliam and Dunford 1980; Richerson and Boyd 1978, 1992; chapters 7–9, 11, and 12, this volume).

A key question that arose within this evolutionary context was, What, exactly, *is* the unit of cultural transmission? Further, how would we know if we found one (Pocklington 2006)? Various names were proposed for units—*menemotype* (Blum 1963), *sociogene* (Swanson 1973), *instruction* (Cloak 1975), *meme* (Aunger 1999, 2002; Blackmore 1999, 2000; Dawkins 1976), and *culturgen* (Lumsden and Wilson 1981)—but there is still considerable debate over what the units embody (Atran 2001; Sperber 1996, 2000). Although perhaps a bit more sophisticated, these debates, with one major exception, are similar to those seen decades earlier with respect to culture traits (Lyman and O'Brien 2003; O'Brien 2007).

The exception concerns the nature of the units of cultural inheritance: Do they have a physical nature similar to genes? No ethnologist or archaeologist of the twentieth century ever assumed that the ideas behind the physical manifestation of culture traits had a physical presence, but some modern researchers in memetics have made that proposal (e.g., Aunger 2002). However, Henrich et al. (2008; see also Boyd and Richerson 1985; Henrich and Boyd 2002) have shown that it is possible to build a valid theory of cultural evolution on Darwinian foundations without assuming particulate inheritance. This is good news for those of us interested in cultural evolution because we can focus on understanding where the units that get culturally transmitted come from in the first place.

Simply because the units of cultural inheritance are not particulate in the same way genes are (assuming this to be the case, at least at the phenomenological level) does not mean that biology is incapable of offering helpful analogues when it comes to understanding the production and transmission of novelties (Eerkens and Lipo 2007; Mesoudi and O'Brien 2009; Shennan 2002b; chapters 3–5, this volume). The key point is that the “calculated heritabilities for human behavioral traits are as high as or higher than measurements for behavioral and other phenotypic characters in natural populations of non-cultural organisms. . . . Thus it may be that [social learning] is as accurate and stable a mechanism of inheritance as genes” (Boyd and Richerson 1985: 55). Even where there is considerable noise in transmission at the individual level, there are powerful evolutionary mechanisms that can lead to stability at the population level (Henrich and Boyd 2002; Henrich et al. 2008).

Innovation, then, becomes a key area of analytical focus in any evolutionary study, especially with respect to the form of the innovation, its composition, and the process that created and maintained it. It is one thing to know how and under what conditions an

innovation is transmitted, but it is a different matter to understand where it came from. Even more important is understanding that, especially with respect to cultural transmission, which is exponentially faster and has less fidelity than biological transmission, the transmission process itself can be a continuous creator of innovation. Much more so than is typically the case in biology, tempo and mode can interact in cultural situations to create a new source of innovation and to create it at scales that may be both large and complex. This undoubtedly is what Trigger (1998: 364) had in mind when he referred to the “unique, emergent aspects of human behavior.”

### *Recipes*

In the social sciences there is a tendency to think of innovations as monolithic entities—the television set, ceramic cooking vessels, and the like. It might be useful, however, to remember that innovations are amalgams of units of varying scale that are linked functionally (and sometimes not [Shennan 2001; chapters 8 and 9, this volume]). One way of viewing innovations is in terms of “recipes” (Lyman and O'Brien 2003; Mesoudi and O'Brien 2008c; Neff 1992)—the materials (“ingredients”) required to construct a tool, for example, and the behavioral rules (“instructions”) required to construct and use the tool. Cognitive psychologists (e.g., Weber et al. 1993) have proposed that people represent tools as interlinked, hierarchical knowledge structures, incorporating behavioral scripts governing their construction and use, much like the recipe concept (Stout et al. 2008). Biologists, too, use the “recipe” metaphor to describe the development of organisms from genetic information (Dalton 2000; Ridley 2003).

Krause (1985: 30–31) was one of the first to employ the concept of “recipe” in a cultural context, defining it as a “list of ingredients and amounts” and a “part that tells you what to do, how to do it, when to do it, and for how long.” Schiffer and Skibo (1987: 597) developed the notion, defining a “recipe for action” as “(1) a list of raw materials, (2) a list of tools and facilities employed, (3) a description of the sequence of specific actions undertaken in the technological process, and (4) the contingent rules used to solve problems that may arise.” They note that recipes are often culturally transmitted, which requires a teaching framework that includes imitation, verbal instruction, hands-on demonstration, and self-teaching by trial and error (see Guglielmino et al. 1995; Shennan and Steele 1999; chapters 10, 13, and 15, this volume).

The concept of recipe is useful for three reasons (Lyman and O'Brien 2003). First, the commonsense meaning of the term captures what anthropologists mean when they use the term “cultural trait”—how, when, where, and why to produce something, whether a behavior or an artifact (a behavioral by-product). Second, the recipe concept contains multiple parts of two general kinds—ingredients and rules—that can be reconfigured to form a different recipe. Any change in ingredient acquisition, preparation, type, or amount; change of rules or the order of their implementation; or some combination of each results in a different product. Third, the recipe concept highlights the flexibility built into virtually

all ways of doing something and still producing a usable product (see chapter 14, this volume).

This again emphasizes the point that units of cultural transmission and replication can be of different scales. In biology, we know the scale of the unit of transmission and replication—the gene—but we also know that there often is no one-to-one correspondence between a gene and a somatic character. One phenotypic character of an organism can be polygenic (influenced by multiple genes), whereas others can be pleiotropic (a single gene influences those several characters). The same applies to cultural transmission, where conceivably every human behavior is underpinned by a recipe of unique composition, scale, and complexity (Lyman and O'Brien 2003).

### ***Dual-Inheritance Theory***

Boyd and Richerson's collective work (e.g., Bettinger et al. 1996; Boyd and Richerson 1985, 1989; Henrich and Boyd 1998; Richerson and Boyd 1992; see also Cavalli-Sforza and Feldman 1973, 1981), often referred to as "dual-inheritance theory" (Richerson and Boyd 1978; Shennan 2002a), is particularly useful here (chapters 5, 7, and 12, this volume). It posits that genes and culture provide separate, though linked, systems of inheritance, variation, and evolutionary change. The spread of cultural information is viewed as being affected by numerous processes, including selection, decision making, and the strength of the transmitters and receivers. However, there is much more to Boyd and Richerson's work than how and why traits spread. Their models also demonstrate that some innovation is produced through the intricacies of the transmission process itself. This calls into question the primacy of selection as the single most important evolutionary process.

We in no way want to remove selection from its prominent place at the evolutionary table. Rather, we point out that an overemphasis on selection as *the* key component of evolution (e.g., O'Brien and Holland 1990) has shifted attention away from adequate consideration of how variation is produced and transmitted and the effects that production and transmission, irrespective of selection, have on evolution (Lipo et al. 1997; O'Brien 2007; Shennan 2001; chapter 8, this volume).

Numerous anthropological studies have made use of models derived at least in part from the work of Boyd and Richerson and their colleagues to examine patterns of cultural transmission in archaeological contexts (e.g., Bentley and Shennan 2003; MacDonald 1998; Shennan and Wilkinson 2001; chapters 7, 9, 11, and 12, this volume), and the variety and complexity of the processes involved is increasingly clear (Shennan 2008a, 2008b). One interesting study of the spread of innovation is Bettinger and Eerkens's (1997, 1999) analysis of stone projectile points from the Great Basin of the western United States. There, the bow and arrow replaced the atlatl (spear thrower) around A.D. 300–600—a replacement documented by a reduction in size of projectile points. The weight and length of points manufactured after A.D. 600, however, was not uniform across the

region. Rosegate points from central Nevada vary little in weight and basal width, whereas specimens from eastern California exhibit significant variation in those two characters. Why are there differences, and what, if anything, do they tell us about the production and spread of innovations?

Bettinger and Eerkens propose that the variation is attributable to differences in how the inhabitants of the two regions obtained and subsequently modified bow-related technology. Bow-and-arrow technology in eastern California was both maintained and perhaps spread initially through what Boyd and Richerson (1985) refer to as *guided variation*, wherein individuals acquire new behaviors by copying existing behaviors and then modifying them through individual and independent trial and error to suit their own needs. Conversely, bow-and-arrow technology in central Nevada was maintained and spread initially through *indirect bias*, in which individuals acquire complex behaviors by opting for a single model on the basis of a particular trait identified as an index of the worth of the behavior (see chapters 7, 11, and 12, this volume).

Bettinger and Eerkens propose that in cases where cultural transmission is modified by guided variation, human behavior will tend to optimize fitness in accordance with the predictions of a cost–benefit model in which individual fitness is the index of success, with little opportunity for the evolution of behaviors that benefit the group as a whole. In instances where transmission is through indirect bias, which tends to produce behaviorally homogeneous local populations, conditions may be ripe for the evolution and persistence of group-beneficial behaviors and cultural group selection (Henrich 2004b). On the other hand, as a result of the disconnection from current local conditions that indirect bias implies, the practice or product may be suboptimal.

From the standpoint of innovation, the models present widely differing scenarios. In both, individuals copy existing behaviors wholesale—innovations can suddenly “appear” in a new region as large, complex packages (e.g., projectile points), perhaps by diffusion—but in guided variation individuals begin tinkering with certain aspects, whereas in indirect bias they do not. Under perhaps extreme conditions, individuals may not even be aware of the underlying principles of how and why something works. All they know is that it *does* work, at least reasonably well, and they attempt to reproduce it in toto. Of course, the copying process itself is rarely faithful, thus presenting plenty of chance for copying errors, which themselves are novelties (Eerkens and Lipo 2005). Whether or not the errors are reproduced, and at what rates, are separate matters entirely.

Theoretical models are powerful tools, and applications of the models to actual data are why we do science, but controlled “middle-range” experiments provide the necessary bridge between the two (Mesoudi 2008a; chapter 11, this volume). In that vein, Mesoudi and O'Brien (2008a, 2008b) designed an experiment to examine the cultural transmission of projectile-point technology, simulating the two transmission modes—indirect bias and guided variation—that Bettinger and Eerkens suggested were responsible for differences in Nevada and California point-attribute correlations.

In brief, groups of participants designed “virtual projectile points” and tested them in “virtual hunting environments” with different phases of learning simulating indirectly biased cultural transmission and independent individual learning. As predicted, periods of cultural transmission were associated with significantly stronger attribute correlations than were periods of individual learning. This obviously has ramifications for how one looks at innovation. In simplified terms, more “loners,” more innovation; more conformist individuals who want packages off the shelf, less innovation. The experiment and subsequent agent-based computer simulations showed that participants who engaged in indirectly biased horizontal cultural transmission outperformed individual-learning controls (individual experimentation), especially in larger groups, when individual learning is costly and the selective environment is multimodal (Mesoudi 2008b; Mesoudi and O’Brien 2008a, 2008b).

Cultural transmission in a multimodal adaptive landscape, where point-design attributes are governed by bimodal fitness functions, yields multiple locally optimal designs of varying fitness (Mesoudi 2008b; chapter 11, this volume). Mesoudi and O’Brien hypothesized that innovations, represented by divergence in point designs resulting from individual experimentation (guided variation), were driven in part by this multimodal adaptive landscape, with different individuals converging by chance on different locally optimal peaks. They then argued that indirectly biased horizontal cultural transmission, where individuals copy the design of the most successful person in their environment, allows individuals to escape from these local optima and jump to the globally optimal peak (or at least the highest peak found by people in that group). Experimental results supported this argument, with participants in groups outperforming individual controls when the group participants were permitted to copy each other’s point designs. This finding is potentially important to the production of innovation, as it demonstrates that the nature of the selective environment will significantly affect aspects of cultural transmission.

How realistic is it to assume the presence of a multimodal adaptive landscape? Boyd and Richerson (1992) argue that multimodal adaptive landscapes are likely to be common in cultural evolution and may significantly affect the historical trajectories of artifact lineages, just as population-genetic models suggest that multimodal adaptive landscapes have been important in biological evolution by guiding historical trajectories of biological lineages (Arnold et al. 2001; Lande 1986; Simpson 1944). Many problems and tasks faced by modern and prehistoric people would have had more than one solution, some better than others, but all better than nothing, and solutions are likely to represent compromises among multiple functions and requirements.

### *Tempo and Mode*

What about the tempo of the jumps across the adaptive landscape? The ethnological and archaeological records are replete with evidence that the tempo of cultural change is rarely constant, but there are few cases in which it has been measured directly (but see Shennan

and Bentley [2008] for changing innovation rates in pottery decoration and Henrich [2004a] for a broader analysis and discussion). Again, how are scale and tempo correlated? Is the apparent rapid emergence of a new form actually sudden, or is it an illusion, meaning that the scale at which we are examining something makes it appear as if the object is new when in actuality it is the product of myriad small-scale cumulative modifications that took place over a relatively long period of time? (See the discussion at the beginning of this chapter and chapter 13, this volume.)

This same question was asked in paleontology for decades. Darwin's notion of the evolution of species was based on gradualism—the slow buildup of small-scale change over geological time—although his theory did not require that tempo. Simpson (1944) opened the door on the notion of accelerated tempo, and Eldredge and Gould (1972; Gould and Eldredge 1977) opened it wider with their concept of *punctuated equilibrium*. They argued that *cladogenesis*—the division of a taxon into itself and at least one sister taxon—is the general mode under which evolution operates (as opposed to *anagenesis*, or the evolution of one taxon into another) and that rapid cladogenesis is orders of magnitude more important than gradualism as a tempo of speciation.

Paleobiologists have erroneously used punctuated equilibrium to model evolution's temporal component, despite warnings from Gould and Eldredge that the model is “a specific claim about speciation and its deployment in geological time; it should not be used as a synonym for any theory of rapid evolutionary change at any scale” (Gould 1982: 84). They issued such warnings to emphasize the cladogenetic aspect of the punctuated-equilibrium model, thus trying to ensure that it was not confused with saltationism—the belief that evolution depends on the appearance of macromutations that exhibit significant disjunctions with their parents (see chapter 4, this volume).

## Discussion

Tempo and mode are only two of the myriad issues that have as yet been inadequately addressed with respect to the origin and spread of cultural innovation, yet they offer exciting entry points into the discussion (Eerkens and Lipo 2007; O'Brien 2005, 2007; O'Brien and Lyman 2000). Whether one views punctuated equilibrium as a particularly useful model in understanding the origin and spread of innovation, there should be no denying that it calls attention to the linkage between tempo and mode. Clearly, by definition, any innovation in a cultural lineage is cladogenetic, creating a new branch in an evolutionary tree. However, these may be on a relatively trivial scale, those characterized by small innovations in pottery decoration, for example, or highly significant, such as subsistence innovations that have a major impact on many aspects of the subsequent trajectory of those who adopt them, differentiating them along many dimensions from the continuing non-innovating branch. Moreover, the second case is likely to be associated with an increased tempo of change, while the first will probably not be.

## Conclusion

Given the exponential growth in the evolutionary literature on both the units of transmission and the processes through which information is transmitted and received, the next decade should witness substantial progress in our understanding of cultural innovation in all its various guises. On a broader plain, evolutionary anthropology has made great strides in developing a body of theory that complements biological evolutionary theory as opposed to borrowing it wholesale and hoping that it contains something of value (Shennan 2000, 2008b; chapter 2, this volume). There is every reason to suspect that this trend will continue, and the chapters in this volume strongly support that claim.

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## Note

1. Of course, the trait in question is indeed the descendant of its specific ancestor; it's just that it now finds itself in a milieu where most of the other traits have different histories of descent.

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