

Phylogenetics and Material Cultural Evolution

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Cultural artefacts, like genes and languages, reflect their history. The methodology of inference of that history, however, has been a contentious question. Recent applications of biological phylogenetic methodology to infer historical patterns of material culture are often explicitly justified on the grounds that essentially similar processes underlie evolution in both biological and material cultural realms. Conventional phylogenetic techniques, while helpful in some cases, do not provide a general theoretical and operational framework for reconstructing material cultural history. Critical analyses of the diversity patterns of two musical instruments, the stringed psaltery and the brasswind cornet, reveal paths of information transfer and the origins of innovation unique to the cultural context that are unlike those in biological systems.

Evolution, “descent with modification,” in Darwin’s original phrase, is not restricted to the biological world and in a broad sense applies to any historical process that rests upon transmission of information from one generation to the next. From this standpoint, human culture undeniably evolves, but to what degree the processes of cultural change mirror biological evolution remains an unsettled question. Do the processes of change in nature and culture resemble each other only superficially, or are they governed by the same fundamental laws? In the context of the broad analogy between biological and cultural processes, an analogy that has been and continues to be instrumental for theoretical development in social sciences (Weingart, Mitchel, et al. 1997), lies the issue of the utility of phylogenetic reconstruction developed originally for biological modes of inheritance. Here we evaluate aspects of cultural transmission relevant to the theory and practice of phylogenetics in the context of material cultural evolution.

The beginning of the new millennium has seen a renaissance of biological metaphors of pattern and process of change in the domain of cultural evolution (Mace and Holden 2005). This renewed interest in rigorous testing of cultural historical hypotheses was initially triggered by growth in the theory of phylogenetic systematics and the increasing sophistication of computerized algorithms in biology (Boyd et al. 1997; Mace, Holden, and Shennan 2005). Application of methodologies

originally formulated for biological questions has earned general acceptance in historical linguistics and stemmatics (historical reconstruction of ancient manuscripts), though the underlying theory had already been developed in these fields prior to the widespread implementation of cladistics in biology (Platnick and Cameron 1977). Subsequently, novel biological probabilistic and network-based phylogenetic approaches, respectively, have been adopted in these fields (Barbrook et al. 1998; Gray and Atkinson 2003). More recently, however, the use of phylogenetics has been extended to encompass a broader array of cultural phenomena, including transformation of material culture (O’Brien, Darwent, and Lyman 2001; Tehrani and Collard 2002; Tëmkin 2004). While the number of empirical studies in this field is still quite small, general claims about the nature of change in material culture have ranged from subsuming culture entirely under the Darwinian framework of the biological world (O’Brien and Lyman 2003; Mesoudi, Whiten, and Laland 2004) to accenting essential differences between biological and material cultural evolution, entailing a more restricted application of traditional phylogenetics (Eldredge 2000; Tëmkin 2004; Eerkens, Bettinger, and McElreath 2005).

Trees of Strings and Valves

Previous attempts to reconstruct phylogenies of cultural artefacts have suffered from a reliance on theory over empirical evidence and have been largely limited to cases with expectedly strong cultural transmission, such as cladistic analyses of Paleoindian projectile points (O’Brien, Darwent, and Lyman 2001) and ornament patterns of Turkmen textiles (Tehrani and Collard 2002). To test more rigorously the applicability of the theoretical assumptions embedded in the methodology of biological systematics in the reconstruction of the history of human artefacts, we assembled large and comprehensive databases on two musical instruments: the cornet (a soprano brasswind instrument) and the Baltic psaltery (a plucked stringed instrument).

Valved cornets appeared some 180 years ago, soon after the development of metallurgical techniques that made it possible to manufacture non-leaking valves (whether piston, rotary, or other early valve types no longer extant). Cornets are orchestral and band instruments that have been in wide use throughout Europe and North America, though they have given way to trumpets as the soprano brasswinds of choice in most regions and musical contexts since the 1920s. The data on cornets consist of more than 600 constructional (organological) descriptions, detailed patent information pertaining to the place and origin of many of the models, and documented transactions among manufacturers. By and large, the entire history of cornets is well documented (Eldredge 2002), providing a unique case to test the performance of phylogenetic methods on actual data with a known true phylogeny.

The earliest physical evidence of the Baltic psaltery dates to the late tenth to early eleventh century (Povetkin 1992; Malinowski 2000), and at least since the Middle Ages the instrument was restricted to adjacent lands of the Baltic States, Finland, and northwestern Russia, where it still survives in remote villages. Prominently featured in folklore, the Baltic psaltery is an integral part of secular and ritual life and has become a national symbol for every ethnic group that has it (Reynolds 1983; Rahkonen 1997; Haas 2001). Unlike manufactured cornets, the psalteries were usually made by individual craftsmen who passed on their skills to apprentices. The data on the psalteries consist of nearly 100 organological descriptions, the geographical distribution of ethnographic and archaeological instruments, and a rich collection of iconographical, folkloristic, and linguistic sources. The historical development of the Baltic psaltery has been a controversial subject for over a century (Haas 2001; Rahkonen 2001; Tëmkin 2004) and, in contrast to cornet history, remains so to this day.

From Tree to Jungle

Given major differences in time scale, ways of manufacture, and social environment, the histories of the two instruments represent very different trajectories of cultural transmission. This enables us not only to assess the relative utility of phylogenetic techniques in unlike cultural contexts but also to compare cultural historical patterns in the hope of gaining insight into the underlying mechanisms of change.

We employed an array of phylogenetic techniques to reconstruct the history of the two instruments, including cladistic and phenetic methods implemented in a standard phylogenetic software package, PAUP* (Swofford 2001) and the network-building algorithms in T-Rex (Makarenkov 2001). Regardless of the methodology and criteria tested, the analyses of the psalteries converged on the topology that recovered several major clades reflecting linguistic relatedness within each group (fig. 1). A close association of the Slavic and Finnic psalteries and a more basal placement of the Baltic psalteries suggest that the musical tradition of building and decorating the instrument closely reflects geographical proximity rather than linguistic affinity (the Slavic and Baltic languages are sister groups within the family of the Indo-European languages [Gray and Atkinson 2003; Rexová, Frynta, and Zrzavý 2003] whereas the Finnic languages belong to the Ural-Altai family of languages [Uralic and Altaic languages 2001–4]). An attempt to apply network-based approaches revealed a large number of reticulations, implicating substantial interlineage information transfer, but this approach was unable to discriminate between recombination and conflicting data, making it difficult to interpret the results. In most instances, however, the linguistically incongruous distribution of psalteries is corroborated by documented instances of extensive cultural exchange. For example, the musical culture of the Setu, a Finnic-speaking ethnic group living in northwestern

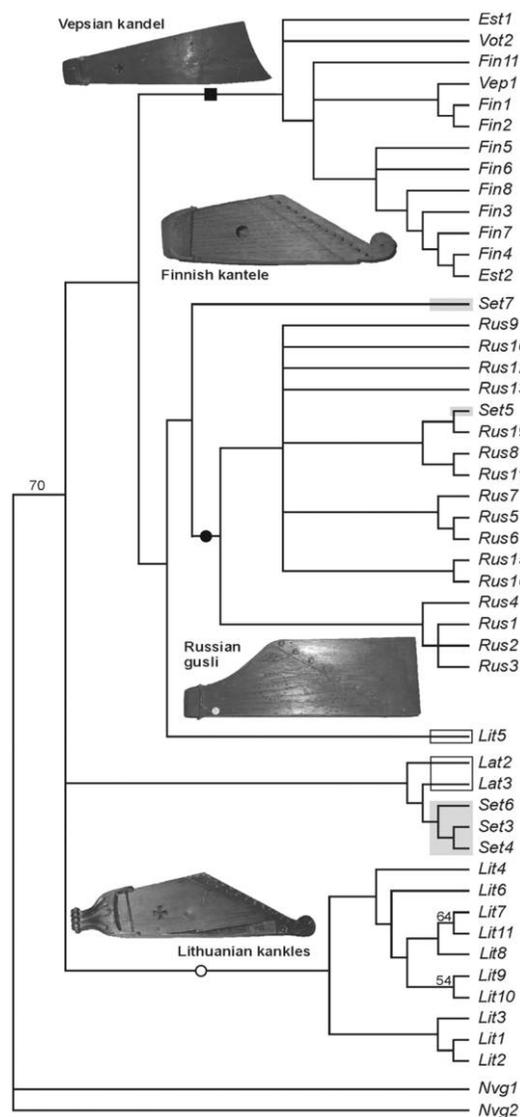


Figure 1. Cladogram of the Baltic psaltery. Majority-rule consensus tree of 4,931 equally parsimonious trees (length = 274, consistency index [excluding uninformative characters] = 0.31, retention index = 0.54) constructed from the maximum parsimony analysis of 59 characters describing each terminal. Circles and squares indicate clades corresponding to linguistic groups. Baltic group (*white circle*): *Lat*, Latvian; *Lit*, Lithuanian; Ural-Altai group (*black square*): *Est*, Estonian; *Fin*, Finnish (including Karelian); *Set*, Setu; *Vep*, Vepsian; *Vot*, Votic; Slavic group (*black circle*): *Rus*, Russian. The tree is rooted with the best-preserved archaeological Baltic psalteries (*Nvg*) excavated in Novgorod, Russia (reviewed in Tëmkin 2004). *White and grey boxes*, Baltic and Finnic psalteries respectively that fall outside the corresponding linguistic groupings. Bootstrap support values are shown above branches (2000 replicates). For a detailed discussion of the cladistic analysis, see Kitching et al. (2000); specific algorithms are described by Felsenstein (2004), and the theoretical basis of the cladistic approach has been thoroughly discussed by Farris (1983).

Russia adjacent to eastern Latvia and southern Estonia, has been greatly influenced by that of their neighbours (Tönurist 1977), as is reflected in the grouping of some Setu instruments with the Slavic and others with the Latvian psalteries. Despite the fact that the phylogenetic results provide the grounds for a meaningful interpretation of the psalteries' origin and diffusion, the pattern of relatedness of the Baltic psalteries suggests a complex history of intercultural contact (Tönurist 1977; Haas 2001; Tëmkin 2004) evidenced by low branch support and a high degree of similarity resulting from convergence, independent parallel changes, and reversals (collectively referred to in biology as homoplasy).

Despite a much more extensive sampling of and detailed information on the cornets, none of the techniques allowed unequivocal reconstruction of their history. The significant extent of information transfer among lineages may account for the fact that phenetic techniques performed better than cladistic methods. As with the psalteries, the network-based approaches identified potential rampant interlineage transfers. A much more comprehensive phylogenetic history was reconstructed by incorporating knowledge of origination and discontinuation (i.e., direct temporal information, the equivalent of using "stratigraphic" information in paleobiology) of the manufacture of various models into network-based phenetic and discrete character-based methods to uncover reticulations in the cornet phylogeny (fig. 2). This synthetic approach provided greater resolution, approximating the "true tree." Nevertheless, several significant nodes were not recovered by the methodology when compared with actual documented history. We believe that the inability of the most sensitive methods to recover the true topology reflects more than simple conflict in phylogenetic signals.

The Quirks of Cultural Transmission

Problems in reconstructing the history of material cultural evolution with biological methods have allowed us to pinpoint some essential differences between evolutionary processes in culture and nature that have largely been overlooked in studies otherwise focusing on the apparent similarities between the two systems.

The most obvious differences are in the frequency and mode of interlineage transfer of information. In the natural world, such reticulations occur primarily in bacteria as a consequence of horizontal gene transfer and during hybridization in eukaryotes (Woese 2000; Andersson 2005). The detection and representation of the so-called complex taxa (hybrids and holobionts) that arise as a result of these processes have proven to be a complex methodological problem requiring a priori knowledge of evolutionary history, though not precluding the use of phylogenetic analysis altogether (Humphries 1983; Nelson 1983; Wagner 1983; Wanntorp 1983; Skála and Zrzavý 1994). In fact, the rapid accumulation of genome-wide DNA sequence data and the growing body of novel analytical approaches promise solutions to the problem

of identifying horizontally transferred genetic material with high fidelity (Baptiste et al. 2005; McInerney and Wilkinson 2005; Beiko and Hamilton 2006; Huang and Gogarten n.d.).

While in biology reticulate evolution is rampant in relatively limited (yet very diverse) domains of the tree of life, recombination in cultural evolution is likely to be a prevalent mechanism of information transfer, with the potential of swamping the phylogenetic signal in the case of particularly wide-ranging exchange of information across cultural "clades." Indeed, it has long been recognized that cultural information can be transmitted in multiple ways (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985, 1987; Durham, Boyd, and Richerson 1997; Richerson and Boyd 1992; Weingart, Boyd, et al. 1997). Reticulation in particular has been widely acknowledged as an important property of cultural transmission (Tylor 1871; Steward 1944; Kroeber 1948) and has been considered a major obstacle to the application of cladistic methods to questions of cultural evolution (Welsch, Terrell, and Nadolski 1992; Moore 1994a, b; Welsch and Terrell 1994; Dewar 1995; Terrell and Stewart 1996; Terrell, Hunt, and Gosden 1997; Terrell 2001). In addition to reticulations in which information flows horizontally among lineages, information also travels through time when "extinct" designs or their elements are reintroduced years or even centuries after they have fallen out of fashion. For example, the short, "shepherd's crook" cornet bell design, an icon of the Victorian era, was virtually extinct after World War I and perhaps wholly so after World War II. A recent wave of nostalgia beginning roughly in the 1980s has brought the shepherd's crook back to prominence in cornet design. Thus, transmission can be ensured even when a cultural lineage is historically discontinuous. There is no counterpart of this process in biological systems: extinction inevitably results in a loss of information. Furthermore, there is a tendency toward increasing intensity of convergence due to intensification of cultural exchange: the increasing popularity of the German zither and the influence of Western classical musical instruments at the turn of the nineteenth century occurred throughout the Baltic area, resulting in independent adoption of many structural elements by different regional forms of the Baltic psalteries. A comparison of the degree of success of standard cladistic methods in reconstructing artefact phylogenies simulated under different modes of cultural transmission has demonstrated that cladistic methods perform well in certain cases but fail in others (Eerkens, Bettinger, and McElreath 2005). Thus, in complex real-world scenarios, the utility of approaches based on hierarchical distribution of shared derived similarities will be determined by the relative frequencies of different modes of cultural transmission.

While reticulation is not unique to cultural evolution (although it has certain unique properties) and the development of methodologies, particularly network-based ones (Lipo 2005), can potentially alleviate the problem of discovery of reticulate phylogenies, other complications stem from the peculiarities of cultural systems.

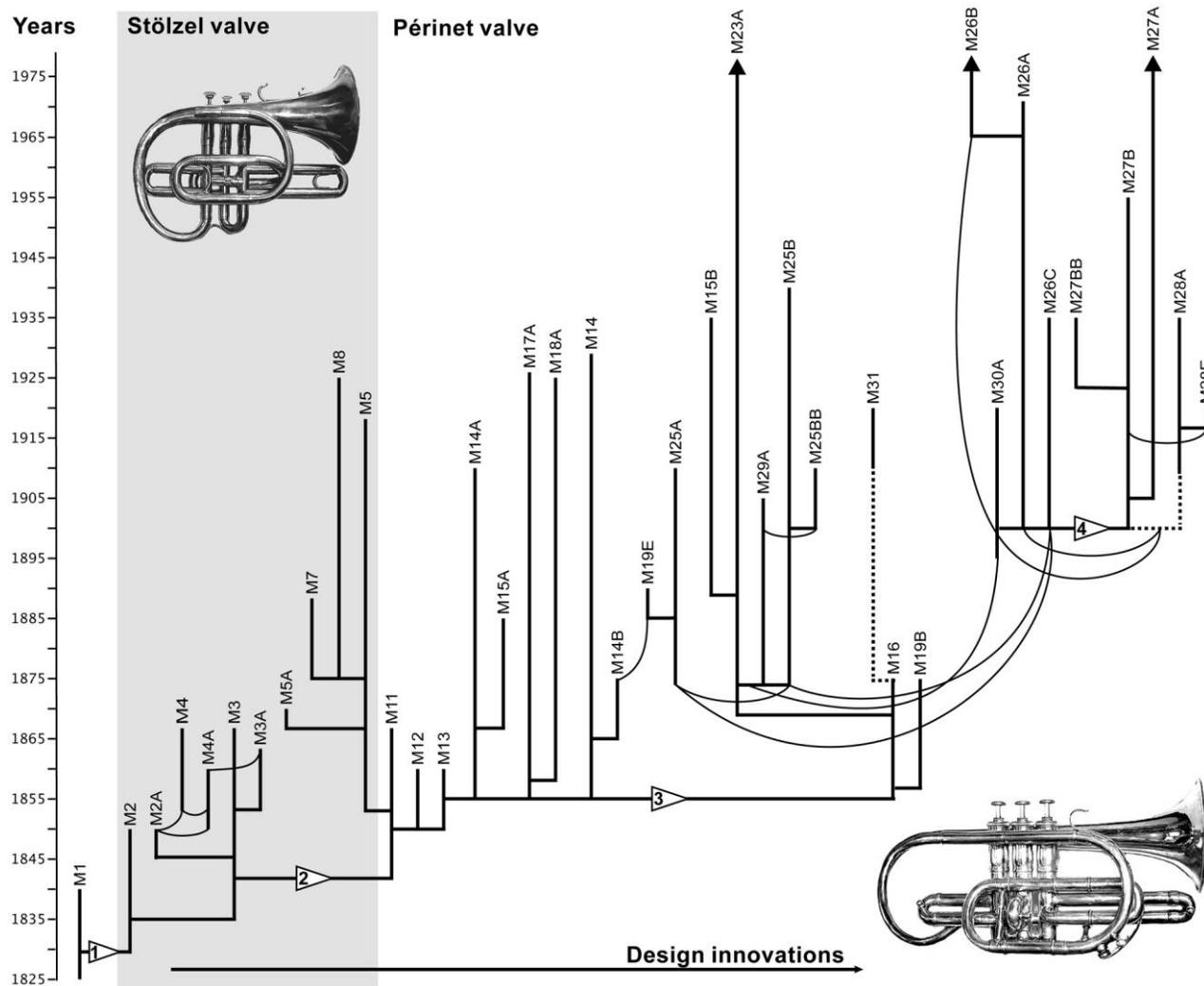


Figure 2. Evolutionary tree of cornets. The relationships among different models (M) are calibrated against the timeline so that the vertical branches correspond to periods of manufacture of particular models. *Shaded left and non-shaded right areas*, instruments equipped with Stölzel and Périnet valve systems respectively. *Curved lines*, reticulations, potential nonvertical instances of information transfer among makers. *Triangles*, key innovations in cornet design: (1) valve number, (2) shifting of the second valve slide and valve alignment, (3) changing of bell exit position and bell placement, and (4) alteration of bell shape (“trumpetization”). This phylogeny was generated by combining several analytical methods. First, three independent phylogenetic analyses were performed on the same data set. The phenetic (length = 45.8; neighbour-joining) and maximum parsimony (length = 44, consistency index [excluding uninformative characters] = 0.4, retention index = 0.8) trees were computed in PAUP* (Swofford 2001), and the reticulate network (based on the dissimilarity matrix generated in PAUP*) was computed in T-Rex (Makarenkov 2001). The reticulate branches generated by T-Rex were subsequently plotted onto the neighbour-joining tree. The reticulate branches suggesting relationships that were not corroborated by the presence of at least a single character in any of the shortest trees in the maximum parsimony analysis were eliminated. Nonsynchronous temporal distribution of sister taxa was interpreted as direct ancestry of a younger model from an older model.

In biology conventional phylogenetic algorithms treat taxa as terminals, the tips of a tree, while actual ancestors are assumed to be hypothetical and not identifiable in practice. That biological ancestors (species) cannot even in principle be identified with existing phylogenetic algorithms is a drawback in the application of such techniques to systems, whether biological or cultural, where there is strong reason to believe that actual ancestors are included in the database. In material culture, for example, there are cases in which a particular artefact was used as a prototype—a direct ancestor. For example, in the course of the “modernization” of the rustic folk instruments by urban enthusiasts at the turn of the twentieth century, a specific version of the Baltic psaltery was developed in Russia that later served as a prototype for the manufacture of a standardized ensemble model that is still played today, while its forerunner became part of a museum collection. Both the psaltery and cornet databases reveal a pattern of well-documented temporally spaced sequences of “missing links” that likely indicate an actual pattern of ancestry and descent.

Another important issue emerges in relation to ancestry: a single artefact can be copied many times, with the result that the tree will not necessarily branch dichotomously but will have bursts of multiple lineages arising from the same node. While such patterns are characteristic in adaptive radiations in biology (often detected as nonresolved “star burst” nodes), their frequency in material culture is likely to be much higher, although recognizing such events in light of a high degree of interlineage reticulation will be problematic.

In addition to the differences in the mode of information transfer in biological and material cultural realms are fundamental differences in the nature of evolving entities themselves. The integrity of the individuals of biological species is ascertained through strictly coordinated ontogenesis the fidelity of which is ensured by a phylogenetic linkage of ancestors and descendants. Although certain stylistic and structural constraints play a role in material objects (for example, adding extra strings to a psaltery results in increased tension that requires a modification of a stringholder mechanism), the level of interdependence of their parts is hardly comparable to that of biological systems. Consequently, elements of artefacts can evolve nearly independently without destroying the integrity of the whole, each producing a distinct genealogy analogous to discrepancies in gene tree topologies derived for the same set of taxa. While this problem in biology can be circumvented by considering a larger number of loci, thereby suppressing idiosyncrasies of each particular locus and recovering a stronger phylogenetic signal, this may pose a serious problem in reconstructing histories of material culture. The ease with which novelties introduced in certain cornet models at certain times and places could be transferred to other, preexisting designs is a case in point. For example, the fad for placing the bell on the left side of the valve cluster, first introduced by the Parisian maker Courtois ca. 1855, took the British market by storm (hence the term “English bell”),

prompting other makers (especially in Britain) to place the bell to the left of the valves on all other forms of cornet design then in existence.

Homology: The Crux of the Problem

Differences run deeper. In the historical development of man-made artefacts, a single technological function can be solved in many ways differing in underlying physical principles. The temporal sequence of alternative designs in material cultural systems, frequently taken as evidence for homologous similarity (Dunnell 1970; Lyman 2001), is often not equivalent to the transformation series made up of ancestral and derived states, the basic underlying assumption built into all biological phylogenetic analytic rubrics. Rather, in material cultural systems, the historical sequence of design innovations consists of a set of alternative solutions to the same functional problem (the “Hannah Principle” [Eldredge 2005]), in some cases prompted by competition or patent protection for competing designs. This challenges the application of biological notion of homology, which, in turn, lies at the core of phylogenetic inference. In material culture, the basis of comparison is in most cases limited to features that perform the same function rather than sharing function and derived form by common ancestry. Thus, entities in question in the biological versus the cultural domain differ ontologically and epistemologically.

A clear illustration of this point is the history of the piston valve used on cornets and other brasswind instruments. The Stölzel valve (ca. 1825 in cornets), a hollow cylinder the same diameter as the neighbouring tubing, admitting the passage of the windway through portions of its length, came first. A decade and a half later, the Périnet valve appeared; it had cylindrical pistons like the earlier Stölzel valve, but in them the windway was conducted by tubing across the width of the (now generally wider) valve. Historians traditionally view the Périnet valve as mechanically superior to the Stölzel valve (there is actually little empirical support for this contention), but though earlier and arguably “less advanced,” the Stölzel valve is not in any meaningful sense “plesiomorphic” to the supposedly more “apomorphic” Périnet valve. The simple reason for this is that the Périnet valve did not derive from the Stölzel valve but rather was an alternative design solution within certain design constraints (i.e., piston-shaped rather than rotary). Most other innovations in cornet design (including the “evolutionary” history of the Périnet valve itself [Eldredge 2003]) fit this description rather than ancestral/descendant, plesiomorphic/apomorphic transition series typical of biological evolutionary systems. Under such circumstances, recognition of “ancestors” in evolving material cultural systems is even more problematic than it is widely considered to be in biological systematics.

Yet, material cultural systems do sometimes show transition sequences of primitive-to-derived states. Certain features of artefacts are related in a way more similar to homologous

structures, particularly in traditional settings where for symbolic or other reasons some functionless traits, such as vestigial handholes in some psalteries, echoing their lyre ancestry (Haas 2001; Tëmkin 2004), and shapes of decorative soundholes associated with pagan symbolism (Rahkonen 1997; Tëmkin 2004), are retained. Trends in the lengthening of the cornet bell through time also conform to the general model of ancestral-to-more-derived conditions.

Conclusion

In contrast to previous attempts to compare the modes of biological and material cultural evolution, this work focuses on differences rather than similarities between the two systems. We believe that, despite apparent similarities in historical patterns, caution is required in interpreting such patterns in a biological evolutionary framework. Traditional phylogenetic analyses have rather limited application for unveiling material cultural phylogenies, performing best in situations where traditional transmission is strong but intercultural exchange is relatively weak, as is the case with most phylogenetic studies of cultural artefacts published to date. Post-industrial-revolution design systems are particularly labyrinthine in the flow of information both between makers and across clades and in the prevalence of the development of alternate states that do not reflect transformation series comparable to those of biological systems. While it is tempting to attribute the patterns we discover in culture to the same causal processes that operate in nature, cultural systems present greater complexity than their biological counterparts and call for the development of novel approaches to historical inference. The study of cornet design provides a vivid example of the intricacy of cultural historical patterns and suggests directions for future methodological and theoretical development. Incorporation of other evidence in addition to character data (such as stratigraphy with fossils and direct historical information in material cultural systems) and the invention of probabilistic methods that would allow estimation of the likelihood of a phylogeny given a specific model of transmission can potentially provide more realistic historical reconstructions. Also, pioneering reticulate network phylogenies complementing the traditionally used dichotomous hierarchical models of relationships promise fruitful results (Lipo 2005). We see this work as suggesting a new perspective with potential impact on our understanding of the evolution of material culture.

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