

‘Total evidence’ in phylogenetic systematics

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Received: 16 January 2008 / Accepted: 15 July 2008
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Abstract Taking its clues from Popperian philosophy of science, cladistics adopted a number of assumptions of the empiricist tradition. These include the identification of a dichotomy between observation reports and theoretical statements and its subsequent abandonment on the basis of the insight that all observation reports are theory-laden. The neglect of the ‘context of discovery’, which is the step of theory (hypothesis) generation. The emphasis on coherentism in the ‘context of justification’, which is the step of evaluation of the relative merits of alternative theories. The appeal to a total evidence approach in phylogenetic inference. And finally, a silence about causation, which results in an instrumentalist approach to phylogeny reconstruction. This paper explores how these empiricist assumptions are embedded in phylogenetic systematics, and why these assumptions are problematic for cladists (or any taxonomists).

Keywords K. R. Popper · Systematics · Total evidence · Direct optimization

Introduction

Early on during the ‘cladistic revolution’ (Hull 1988), Gary Nelson and Norman Platnick—both at the American Museum of Natural History—asked David Hull to suggest a self-contained book on philosophy of science. His suggestion was Popper (Hull, in lit., 12/22/02). The result was a series of book reviews by Platnick and Gaffney (1977, 1978a, b) “intended expressly for the purpose of informing systematists about relevant ideas in Popper’s works” (Gaffney 1979, p. 105). Platnick and Gaffney (1977) did “not wish to imply that systematists have been

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totally ignorant of Popper and the hypothetico-deductive theory of science.” Instead, their intention was to “encourage this trend”, which was to cast cladistics in the falsificationist mode of hypothetico-deductivism. In his influential textbook on phylogenetic systematics, Wiley (1981, p. 20) claimed to have adopted “the hypothetico-deductive approach throughout”, and recommended the works of Carl Hempel, Karl Popper, and Rom Harré as further reading.

The classical model of scientific explanation under a hypothetico-deductivist paradigm is the deductive-nomological (D-N) model developed by Hempel (1965, 1966). Popper (1935) had already espoused a deductively structured covering-law model of scientific explanation, although he did not formalize it as explicitly as did Hempel and Oppenheim (1948). Even if not applicable to phylogenetic systematics (Sober 1988), the hypothetico-deductively structured covering-law model of scientific explanation exerted a major influence on the theory and practice in cladistics in two respects.

First, as was emphasized by Popper (1935), hypothetico-deductivism allows ignorance about the source of the law (theory, hypothesis) to be tested (Lipton 2004, p. 15). For Reichenbach (1938), the initial conjecture of a testable theory depends on intuition, inspiration, or lucky guesswork, and hence represents a step in scientific reasoning that is not amenable to philosophical analysis (Newton-Smith 1981 [1994], p. 126). The D-N model accordingly ignores this ‘context of discovery’.

The second aspect of the D-N model that gained importance for cladistics is that it allows silence about causation. Hempel (1965, p. 352) explicitly acknowledged: “D-N explanations are not always causal.” He (Hempel 1965, p. 352) used the mathematical relationship between the length and the period of a pendulum as an example of how D-N explanations can be based on “*laws of coexistence*, in contradistinction to *laws of succession*, which concern temporal changes in a system.” According to Hempel (1965, p. 146), a ‘natural’ classification is distinguished from an ‘artificial’ one by the fact that “those characteristics of the elements which serve as criteria of membership in a given class are associated, universally or with a high probability, with more or less extensive clusters of other characteristics.” In his explication of ‘systematic morphology’, Mainx (1955 [1971], p. 580) spoke of a “law of coexistence of characters, which is empirically testable.” Indeed, cladistic analysis tests the ‘coexistence of characters’ on the basis of their congruence relative to a nested hierarchy of taxa (Patterson 1982a).

Cladistic reflections on hypothetico-deductivism

Platnick and Gaffney (1977) highlighted Popper’s insight that theory-free observation is impossible, that all observation reports therefore are open to future criticism and revision (e.g., Platnick 1985, p. 88). This insight turns observation reports into low-level hypotheses (Popper 1935), rather than brute recordings of sense perceptions. Yet the hypothetico-deductive method does not consider the context of theory generation relevant. Characters used in phylogenetic analysis are conjectured, irrespective of their source, then explained as homologues (due to

common ancestry) if they pass the test of congruence. Paraphrasing Hempel (1965), characters are explained as homologous not on the basis of causal processes (of inheritance, development, etc.), but on the basis of their co-existence in a pattern congruent with a nested hierarchy. It is the ‘law of coexistence’ instantiated by character distribution that reveals systematic patterns, and without such patterns, “there is absolutely nothing in evolutionary biology for any causal theory to explain” (Platnick 1982, p. 283).

Beatty’s (1982) discussion of the perils of such an a-theoretical approach to pattern reconstruction (see also Hull 1988; Williams 1992) triggered a flurry of responses from cladists (Platnick 1982; Patterson 1982b; Brady 1982), who insisted on keeping the search for systematic patterns free of theoretical (causal) considerations. According to Platnick (1982, p. 283):

one needs no causal theory to observe that of all the millions of species of organisms in the world, only about 5,000 of them have abdominal spinnerets. One also needs no causal theory to observe that of all the millions of species of organisms in the world, only about 5,000 of them have males with pedipalps modified for sperm transfer ... one needs no causal theory to observe that such massive congruence of characters leaves no reasonable doubt that spiders constitute a real group that actually exists in the present-day world. After all, we would accept the hypothesis that some table exists for exactly the same reason: we can keep bumping into it (i.e., congruence of evidence).

To bump into a table—repeatedly or not—means to enter into a causal interaction with it. Similarly, to call spider male pedipalps ‘transformed for sperm transfer’ implies a causal (functional) grounding of this character. When Hull (1988, p. 491) highlighted these issues, Farris and Platnick (1989, p. 309) responded: “Certainly, no Popperian ever thought that there might exist a ‘theory-neutral observation language’”. However, the issue at stake is not the theory—ladenness of observation, but rather the causal grounding of cladistic analysis.

The requirement for total evidence

In his classic writing on the nature of scientific explanation, Hempel (1965, 1966) introduced two basic models, both characterized as ‘inferential’ by Salmon (1998) because neither requires causal relations. The D-N model requires the deductive entailment of the explanandum by the explanans, which must include the statement of at least one universal law of nature. The D-N model is too strong for phylogenetic systematics (Sober 1988; Rieppel et al. 2006; Vogt 2008), as indeed it may be for other empirical sciences as well.

The alternative to the D-N model developed by Hempel (1965) is the ‘inductive statistical’ (I-S) model of scientific explanation, where the explanandum is expected to obtain with high probability given the premises that constitute the explanans. To ensure a *strong* inductive argument, the I-S model was coupled with the requirement for ‘total evidence’, which is automatically fulfilled for the D-N model. The ‘principle of total evidence’ (Carnap 1950) requires that all *relevant* (Hempel 1965,

p. 64; Salmon 1998, p. 96) evidence be considered for proper inductive inference. ‘Total evidence’ was first introduced into systematics by Kluge (1989) in an argument directed against differential character weighting (considering some characters as more important than others, and weighing them accordingly), data set partitioning (the partitioning of the total available evidence into several data sets that are analyzed separately), and the *a priori* dismissal of any part of the evidence (of both old and new evidence).

However, Popper (1963 [1997], p. 220) denied that scientific theories should aim for high probability, and—in contrast to cladistic practice—requested that old and new evidence be kept separate, and that only new evidence, introduced in a new test of a theory, be allowed to contribute to its degree of corroboration, whereas the old evidence should be relegated to background knowledge (Popper 1963 [1997], p. 221). Acceptance of the principle of ‘total evidence’ thus created an inconsistency for Popperian systematists, who reject an inductivist/probabilistic account of systematics and appeal to ‘total evidence’ not in terms of ‘degrees of confirmation’ of a scientific theory (hypothesis of relationships), but in terms of Popperian explanatory power (Kluge 2001, 2004; Faith and Trueman 2001). The question thus arises how cladists of a Popperian brand justify their appeal to the principle of total evidence in phylogenetic inference?

The nature of evidence in phylogeny reconstruction

Popperian systematists who try to cast phylogeny reconstruction in a hypothetico-deductive framework point to the fact that for any finite number of terminal taxa there exists a potentially very large, but always finite class of possible cladograms (Felsenstein 1978; Wheeler et al. 2006). For example, for three taxa there exist three, and only three, hypotheses of grouping, i.e., hypotheses of relationships: ((A, B) C), ((A, C) B), and ((C, B) A). The class of all possible cladograms obtains through the exhaustive logical permutation of all possible sister-group relationships for all taxa under consideration, such that for any number of taxa, all possible trees are said to exist *a priori* in logical space. Taxonomic characters are then said to choose from among those trees the one(s) with respect to which their distribution amongst the terminals is maximally congruent under some optimality criterion such as parsimony, or under some likelihood model. This is how taxonomic characters are portrayed to ‘test’ alternative phylogenetic hypotheses, a process that was formalized in the form of a *modus tollens* argument (Kluge 2003a).

The *modus tollens* is an argument scheme that is H-D in nature, which requires the *explanans* to logically entail the *explanandum*. Its application to phylogenetic inference would therefore require the possibility of distinguishing *true* homology (similarity due to common ancestry) from non-homology, i.e., homoplasy (Ball 1982; Rieppel et al. 2006). This requirement is too strong for systematics, because there is no deductive link between a hypothesis of relationships and the character distribution on a corresponding tree (Sober 1988). Nevertheless, the argument seems straightforward. Alternative phylogenetic trees are hypotheses under test, the characters are what test these hypotheses. The ‘characters’ are formulated by

systematists as observation reports that translate into character statements with propositional content (Rieppel 2004a; Sereno 2007). If to have a red tail is a possible diagnostic feature of a group of birds, then the statement 'this bird has a red tail' implies the possible homology of the red tail in this and other birds. Since Popper denied the possibility of theory-free observation, such character statements are low-level hypotheses that have to be provisionally accepted by the scientific community if used in a test. But to provisionally accept such defeasible statements as true amounts to Popper's (1935, p. 29) 'harmless dogmatism', harmless because the character statements can themselves be subjected to tests. The question then arises: characters and their distribution test alternative trees, but what tests character statements themselves?

Since character statements are low-level hypotheses, yet the source of hypotheses is considered irrelevant as long as they are testable, there is apparently no need to worry about the origin of character statements. In order to avoid the threat of 'authoritarianism' (Gaffney 1979, p. 104) with respect to the origin of character statements, cladists accord logical priority to the tree, not the characters (Härlin 1999; Ramirez 2007): the validity of character statements becomes tree-dependent, rather than observer-dependent. Characters are not used to build a tree; congruence "of any set of characters" (Härlin 1999, p. 499) helps to identify the preferred (most parsimonious) tree in the set of all possible ones. In Fig. 1, characters 1 and 2 show a conflicting distribution, such that no choice from the three possible trees can be made. Congruence within character set (1, 2, 3) supports the grouping ((A, B) C): this tree implies homology for characters 2 and 3, and homoplasy for character 1. The addition of character 3, and its congruence with character 2, led to the rejection of possible homology for character 1. Congruence in the character set (1, 2, 3, 4, 5) supports the grouping (A (B, C)). The conjecture of possible homology for characters 2 and 3 was tested, and refuted, by the addition of characters 4 and 5, and their congruence with character 1. This is how characters are said to test each other reciprocally under the 'law of coexistence' (Rieppel 2004b). Characters that map

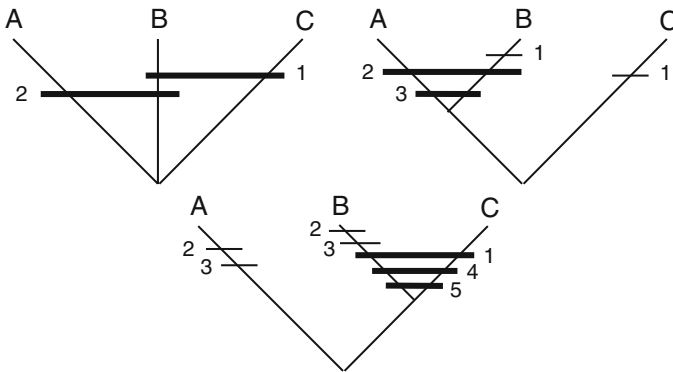


Fig. 1 Three steps in the analysis of the phylogenetic relationships of three taxa, A, B, and C. The first step considers characters 1 and 2; the second step considers characters 1, 2, and 3; the third step considers characters 1, 2, 3, 4, and 5. See text for further discussion

congruently on the preferred, e.g., the most parsimonious tree, are interpreted as homologues i.e., explained by common ancestry. Those that map incongruently on the preferred tree are interpreted as homoplastic (non-homologous), i.e., explained as convergences, reversals, or mistakes made by the observer.

Since ‘character statements’ are treated as defeasible low-level hypotheses, the falsification of such a statement in logical space does not also imply its actual falsity (Popper 1974). This enables Popperian cladists to claim that as new characters are added to the phylogenetic analysis of a set of taxa, relative support (Nixon and Carpenter 1996), or degree of corroboration (Kluge 1997a, b, 2001), for alternative trees may change, turning yesterday’s homologies into today’s homoplasies *and vice versa*—as is licensed by ‘sophisticated falsificationism’ (Farris 1983; Kluge 1997a, b). This, in turn, means that the more characters are entered into an analysis, the more severe is the test of alternative trees, but also of alternative hypotheses of homology. Hence the requirement of total evidence (Kluge 1989), i.e., the requirement that all characters available at the time of analysis, including previously published ones (O’Leary et al. 2003), be entered into the analysis. With all the evidence included in the analysis, the explanatory power of the phylogenetic hypothesis is said to be maximized, either in terms of explaining the largest possible number of shared characters as homologous, or, on a falsificationist account, by minimizing the number of *ad hoc* hypotheses of homoplasy (of rejected hypotheses of putative homology: Farris 1983; Kluge 1997a, b).

The fluidity of character statements

“Assume nothing—it will all come out in a wash” became the new, if unofficial, paradigm of cladistic analysis under the requirement of total evidence. It is not the source of character statements that matters. Instead, it is the degree of mutual coherence, i.e., non-contradiction of character statements relative to a nested hierarchy of taxa that identifies the most parsimonious tree. On a strong reading of Popper (1935), there is no dichotomy between theoretical statements and observation statements (basic statements). Because all observation statements are theory-laden, it can only be the coherence of its constituent statements and postulates that justifies any scientific knowledge claim.

In the interest of avoiding any ‘authoritarianism’ with respect to statements on phylogenetically informative characters (Kearney and Rieppel 2006a), cladists’ rhetoric adopts the very concept of a theory-free observation report that Popper (1935) had criticized: “Operationally, systematics proceeds by gathering data (observations) from organisms and coding them into evidence to test competing phylogenetic scenarios” (Wheeler et al. 2006, p. 7). In contrast, Popper (1974) touted his rejection of the observation/theory dichotomy as his anti-positivist trademark (Newton-Smith 1981 [1994], p. 155). Although cladists pay lip-service to the insight that all observation is theory-laden (e.g., Kluge 2003b), they claim that considerations of inheritance, development, or function, which could influence the choice of characters, are epistemically inaccessible prior to pattern analysis and hence have to be ignored (Platnick 1982), or else burden phylogenetic analysis with

additional assumptions that are unnecessary (O’Leary et al. 2003). Character statements *qua* low-level hypotheses are not critically evaluated with respect to the causal role the characters play in shaping the organism, but only relative to all other character statements entered into the analysis, and the degree of congruence with which they support a certain tree (Nixon and Carpenter 1996), or corroborate it (Kluge 1997a, b).

Under such premises, a special branch of science such as systematics becomes a fluid system of statements, some theoretical (deploying theoretical terms), some observational (deploying observational terms), if such a dichotomy is to be drawn at all (Scheffler 1982). Within that system, no character statement can be considered privileged over any other, all carry equal weight. Should new theoretical, or observational, input generate incoherence within the system, thus prompting its revision, every one of the statements, both observational and theoretical, stands a chance of rejection. To maintain or re-establish coherence, observational statements might prompt the rejection of theoretical statements with the same authority that could justify the rejection of an observation statement in the light of theory. Cladists who reject any theoretical input into character analysis are left with a fluid system of character statements every one of which carries equal weight, and any one of which is open to rejection or revision in search of greater coherence (congruence) relative to a hierarchy of taxa.

Trees versus characters

In order to keep character analysis free of “special pleading for particular characters” (Frost et al. 2007, p. 6) on grounds of theories of inheritance, development, or function, cladists accord logical priority not to character analysis, but to cladograms (Härlin 1999; Ramirez 2007). But cladograms are theories (of phylogenetic relationships) as well, and consequently can import theoretical burden into character analysis ‘from the other end’, so to speak. The resulting fluidity of character statements is here briefly exemplified with respect to a controversy surrounding the origin of snakes (Rieppel and Kearney 2001).

In the late 1970ies, fossils of a marine species of snake with well-developed hind limbs called *Pachyrhachis problematicus* were found in mid-Cretaceous deposits from the Middle East (Haas 1979, 1980a, b; Caldwell and Lee 1997). These fossils quickly became the textbook example for “almost ideal intermediates” between Cretaceous marine lizards, the mosasauroids, and snakes (Carroll 1988, p. 236). Cope (1869, 1872, 1878) had already defended the origin of snakes from mosasaurs. The derivation of snakes from mosasauroids (Caldwell and Lee 1997) is highly contested (Tchernov et al. 2000; Greene and Cundall 2000; Apesteguía and Zaher 2006; Conrad 2008), yet the motivation for a preferred theory can run very deep, and exert theoretical pressure on anatomical interpretations and the resulting character statements.

Kauffmann and Kesling (1960) described an ammonite that they claimed to show marks of 16 mosasaur bites. However, experiments conducted with *Nautilus*, the closest living relative of the extinct ammonoids, showed that mosasaur bites would

not have left puncture holes with smooth edges in a brittle ammonite shell. The bite mark would either have jagged edges, or if forceful enough, the bite would have caused the shell to collapse (Kase et al. 1998). The conclusion was that the alleged mosasaur bite marks in fact represent limpet snail (patellogastropod) home sites (Kase et al. 1994; 1995; Westermann and Hewitt 1995). The ‘smoking gun’ that clinched this explanation (Cleland 2002) was the discovery of corresponding home site marks on the inside of the body chamber of a Cretaceous ammonite, associated with radula scrape marks and with a limpet shell (Seilacher 1998). Under pressure from the theoretical preconception that snakes are descended from mosasauroids, however, Lee et al. (1999) used the putative mosasaur bite marks on the ammonite first described by Kauffman and Kesling (1960) to reconstruct jaw movements in mosasaurs. Their conclusion was that the jaw movements of mosasaurs corresponded to a pattern that is intermediate between that of terrestrial lizards and snakes such as pythons.

This is a functional causal explanation of how feeding mechanics changed in the transition from lizards to snakes via mosasaurs. According to cladistic theory, such a causal explanation requires the prior establishment of a sister-group relationship of snakes with mosasaurs on the basis of character congruence (Platnick 1982). Since the source of character statements is considered irrelevant, and since character statements are tested on the basis of their coherence only relative to a tree topology, preference for a phylogenetic theory can exert significant theoretical pressure on character statements. The following example documents the fluidity of a character statement that is under pressure from a preconceived sister-group relationship of snakes and mosasaurs.

The closest living relatives of mosasauroids are the varanoid lizards, i.e., the monitor lizards (*Varanus*), the earless monitor (*Lanthanotus*), the beaded lizard and the gila monster (*Heloderma*). These varanoids were found to be unique amongst extant reptiles in that they show a complex infolding of the dentine into their pulp cavity (plicidentine: Odermatt 1940; Bullet 1942; Rieppel 1978). Absent in all mosasauroids and in all snakes (Kearney and Rieppel 2006b), this is an *internal* character of varanoid teeth, but the folding of the dentine into the pulp cavity is revealed superficially by grooves near the base of the tooth. In the first comprehensive cladistic analysis of squamate interrelationships, the character statement relating to that condition read: “basal infolding of marginal teeth: (0) not striated; (1) dentine infolded, producing striations” (Estes et al. 1988, p. 132; character 86).

In Lee’s (1997, p. 71; character 88) analysis of varanoid interrelationships this character became: “*Plicidentine* (infoldings of dentine at the base of teeth, forming striations). Absent or weak, 0. Strong, 1. All basal alethinophidians lack plicidentine, although it occurs in some acrochordids and colubrids (see Vaeth et al. 1985).” The point here is that plicidentine refers to a basal infolding of dentine subdividing the pulp cavity *internally*, whereas Vaeth et al. (1985) described the development of superficial enamel ridges, i.e., the ‘fluting’ of the *external* enamel surface on the teeth of some piscivorous higher snakes that has no effect on the dentine and the inner structure of the tooth. This character statement thus reveals a tendency to treat internal and external features of squamate teeth as the same

character, as is again the case in a later incarnation of the same character statement (Lee 1998, p. 400): “148. *Bases of marginal teeth*. Smooth, dentine not infolded (0); dentine infolded (‘plicidentine’), resulting in longitudinal grooves (1) ... *Pachyrhachis* exhibits weak infolding (Lee and Caldwell 1998) and has been coded with state 1”. Yet in their re-description of this marine fossil snake with well-developed hind limbs, Lee and Caldwell (1998, p. 1537) noted that the marginal teeth are “hollow cones” with “very weak grooves ... near the base of each tooth.” The observation, therefore, is not one of infolded dentine, but of weak superficial striation of the enamel surface. Yet by treating those two conditions as the same character, it was now possible to relate snakes to varanoid lizards and their marine fossil relatives, the mosasaurs, by having the derived condition coded as present in extant varanoids, in mosasaurs (where some species have teeth with a ridged enamel surface), and in the textbook intermediate fossil snake.

As the debate on the origin of snakes continued, the same character statement was once again modified in such a way that the term ‘plicidentine’ finally disappeared (Lee and Scanlon 2002, p. 371): “172. External grooves and ridges on tooth bases. 0, present, surface of bases of mature tooth crowns with vertical ridges and grooves. 1, absent, surface of bases of mature tooth crowns smooth.” The presence of vertical ridges and/or grooves on the surface of the teeth continued to support a varanoid—mosasauroid—snake clade in spite of the fact that their developmental origin (Kearney and Rieppel 2006b), as well as their function (compare Vaeth et al. 1985, with Rieppel 1979), is different in extant varanoids as opposed to mosasaurs and snakes. But that is considered not to be a problem, for under the current cladistic paradigm, the validity of character statements turns on their coherence relative to a tree topology and nothing else. However, if one character statement can come under theoretical pressure from a preconceived hypothesis of relationships, then others can come under similar, indeed congruent, pressure.

Cladograms are theories, and theories do not exist in isolation, nor do observation statements: “If observation is ‘theory laden’, theory is ‘observation laden’” (Barnes et al. 1996, p. 92). Both are embedded in a coherent system of thought, which can determine what observations are deemed important in the light of theory, and what theory is deemed acceptable in the light of observation. Cladists may refrain from the causal grounding of character statements in theories of inheritance, development, or function, but that does not mean that character statements cannot come under theoretical pressure from theories about phylogeny.

Taking the subject out of the equation

As is shown by the above example, cladistic methodology has cleansed neither pattern analysis, nor the functional explanation of patterns, from theoretical pressure. This *desideratum* is claimed to obtain through ‘direct optimization’ techniques, originally applied to molecular (DNA) data sets (Wheeler 1998, 2001a, b, 2003a, b, 2005; Wheeler et al. 2006).

In comparative biology, homology is the relation indicative of common ancestry. Under the cladistic paradigm, the conjecture of a homology relation is minimally a

two-step procedure: in a first step, anatomical relations, or relations between base pairs of DNA strands, are established that are conjectured to be homologous in the organisms under analysis. These are the ‘topological correspondence’ relations of Rieppel (1988), or the ‘primary homologies’ of DePinna (1991), i.e., the character statements that are coded into a data matrix. In a second step, these conjectures of homology are tested for congruence relative to (ideally) the class of all cladograms possible for the terminal taxa under analysis (Patterson 1982a). The congruent characters will then be explained as homologies, as due to common ancestry, whereas the remainder, incongruent characters will be considered non-homologous (homoplastic). Crucially, the data matrix that represents the initial conjectures of homology is held constant, i.e., is not allowed to change in order to achieve a greater degree of congruence relative to one or another tree topology during the analysis. But as the example of ‘plicitentine’ discussed above shows, it is possible to re-code a data matrix on the basis of changed character statements for future analysis.

The second step in cladistic character analysis, i.e., the test of congruence (Patterson 1982a), is based on purely logical relations: it examines the mutual coherence or in-coherence of character statements relative to a nested tree topology. The test of congruence (Patterson 1982a) maximizes the relations of inclusion versus exclusion (on congruent characters) and minimizes the relation of overlap (on incongruent characters) between the groups (taxa) that constitute the hierarchy. Since these are purely logical relations, it is only the first step of character analysis, i.e., the formulation of primary homology statements (the construction of the data matrix), which is vulnerable to theoretical pressure. To immunize pattern analysis from theoretical preconceptions, the first step of homology assessment must be eliminated—which is exactly how direct optimization techniques operate (Wheeler 1998, 2001a, b, 2003a, b, 2005; Wheeler et al. 2006).

In traditional molecular systematics, tree-independent sequence alignment yields primary statements (conjectures) of homology, which are then held constant (as entered into the data matrix) in the search for the most parsimonious (or most likely) tree amongst those possible for a given set of taxa. Using direct optimization, homology becomes a ‘dynamic’ (fluid) relation, as sequences are re-aligned during the analysis relative to (ideally) all of the hypotheses of relationships that are possible for the chosen taxa in search for overall maximum parsimony (or maximum likelihood). “Direct optimization simultaneously evaluates nucleic acid sequence homologies and cladograms. The relation of homology thus becomes entirely cladogram-dependent” (Wheeler 2005, p. 71). The number of terminal taxa defines the set of all possible tree topologies, the number and lengths of the DNA strands sequenced define the set of all possible homologies (as they would obtain from all possible alignments) (Grant and Kluge 2004). Direct optimization seeks maximal overlap between these two sets, as it allows the algorithm to re-write the data matrix (to re-align the same sequences) relative to (ideally) each tree topology that is possible for all the taxa under analysis in search for maximum global parsimony. Phylogenetic analysis thus proceeds as a dynamic and reciprocally informative search for maximum overlap of the set of all possible trees with the set of all possible homologies.

Critics of the direct optimization techniques used in sequence alignment deplore a lack of concern for biological considerations in terms of DNA function and

sequence evolution (e.g., Simmons and Ochoterena 2000; Philippe et al. 2005). Metaphorically speaking, nothing would stop direct optimization techniques from potentially aligning features of the humerus with those of the femur in conjectures of homology. Further criticism concerns the application of the parsimony principle in sequence alignment. The appeal to parsimony in traditional phylogenetic analysis has been criticized for implying the assumption that nature is simple, that evolution is a parsimonious process, or that homoplasy is rare. Farris (1983), and Sober (1983, 1988) have shown that these concerns are unwarranted. This is not the case if sequence alignment that specifies molecular homologies is itself optimized under global tree-based parsimony, which minimizes the number of transformation steps relative to a tree topology: "This approach assumes that [sequence] evolution is parsimonious" (Simmons 2004, p. 875). Such a claim seems difficult to defend in light of the radical contingency of the evolutionary process. Furthermore, simulation studies showed that direct optimization does not yield more accurate results than traditional methods of DNA sequence alignment (Ogden and Rosenberg 2007), even if these are rejected as 'subjective' or 'logically inconsistent' (Wheeler et al. 2006).

The cladogram is reduced to the best possible way to organize the given [sequence] data under some optimality criterion, such as parsimony. But the claim that nature itself should be parsimonious is difficult to defend without begging the question (Sober 2006, p. 435). At that juncture, practitioners of dynamic optimization appear to not only adopt the logical empiricists "silence about causation" (Rosenberg 2005, p. 32), but with it the empiricists' leanings towards an instrumentalist outlook (in systematics; Rieppel 2007).

Conclusions

Cladists hoped to purge the influence of theoretical preconceptions in phylogeny reconstruction first by according logical priority to the cladogram (tree) rather than the characters (Härlin 1999), later by eliminating the first step in character analysis, which is the conjecture of primary homologies (*sensu* DePinna 1991), by making the homology relation amongst characters entirely tree-dependent for both molecular (Wheeler et al. 2006), and morphological (Ramirez 2007) data. This leaves congruence, i.e., the coherence or in-coherence of 'fluid' character statements relative to a tree topology, to do all the work in sorting homology from non-homology. The relation of homology is thereby tested on the 'law of coexistence' which requires no appeal to underlying causal relations. If, on this account, an appeal to causality is made, such causality can only consist in the statistically relevant co-occurrence of characters relative to some optimality criterion. The appeal to total evidence in this context serves to boost the justification for the acceptance of a phylogenetic hypothesis, be that in terms of 'support' (Nixon and Carpenter 1996), or some non-Popperian understanding of 'relative degree of corroboration' (Kluge 1997a, b, 2004).

There is little doubt that coherence of character statements relative to a nested hierarchy of taxa is a necessary condition for phylogeny reconstruction, but it is not also a sufficient condition (Kearney and Rieppel 2006a). The reason is the 'fluidity'

of character statements relative to alternative trees. There is also little reason to reject the ‘total evidence’ requirement, although there is no reason not to pragmatically balance it against conditional data set partitioning (the variable partition of the total evidence into different sub-sets of data to be analyzed separately), which can offer important insights into the disjunctiveness or coherence of sub-sets of character statements (Miyamoto and Fitch 1995; Scotland et al. 2003). The major problem with the ‘total evidence’ requirement, however, is the nature of that evidence. Evidence in support of inductive inference needs to be evidence “of an appropriate sort” (Salmon 1998, p. 305), i.e., evidence relevant to the hypothesis (of phylogenetic relationships) under evaluation. However vexing the problem may be for logicians, white tennis shoes have no relevance for the biologist in support of the statement that all ravens are black.

Homology is a relation (the relation of common ancestry); homologues are parts of organisms that participate in this relation. To call parts of two or more organisms homologues means to reify the relation of homology. The proper way to do that is by causal grounding of phylogenetically informative characters in mechanisms of inheritance, development and/or function (Rieppel and Kearney 2007). A “cavalier attitude towards character study” (Jenner 2004, p. 301) will not do, nor the direct optimization of fluid character statements relative to a tree.

Acknowledgments I thank Shannon Hackett, Maureen Kearney, Peter Makovicky, Leo Smith and Nathan Smith for various opportunities to discuss direct optimization techniques in molecular systematics. I also thank an anonymous reviewer of earlier drafts of this paper, and the Editor K. Sterelny, whose comments improved its contents.

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