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HYPOTHETICO-DEDUCTIVISM IN SYSTEMATICS: FACT OR FICTION?

OLIVIER RIEPPEL¹

ABSTRACT

Phylogenetic systematics (the cladistic analysis of phylogenetic relationships) is not hypothetico-deductively structured (in the sense of a covering law model of scientific explanation). If it were, there would be no reason to call for total evidence, since that requirement is automatically satisfied in a deductively structured explanation. Instead, the appeal to the requirement of total evidence in phylogenetic systematics indicates that phylogenetic inference is inductively, or abductively, structured. The principle of total evidence has been invoked to render inductive inference an argument as strong as it can be, but for this to be the case the total evidence must also be relevant evidence, i.e., evidence 'of the right sort' relative to the state of affairs to be explained. Character congruence is a necessary condition for phylogenetic inference, but not also a sufficient condition. What is required in addition is the causal grounding of character statements in theories of inheritance, development and function.

KEYWORDS: Hempel, Popper, cladistics, hypothetico-deductivism, total evidence, relevant evidence.

INTRODUCTION

'An Introduction to the Logic of Phylogeny Reconstruction' is how Gaffney (1979) titled his influential article in which he sketched a hypothetico-deductive approach to the cladistic analysis of phylogenetic relationships. This title, of course, resonated Popper's (1959 [1992]) 'The Logic of Scientific Discovery'. Gaffney (1979: 104) found in Popper's philosophy of science a means to eradicate "nonscientific (non-testable) elements" in systematics, such as "tradition, stability, authoritarianism". In a series of reviews of books by Popper and on Popper, Platnick & Gaffney (1977, 1978a, 1978b) sought to inform "systematists about relevant ideas in Popper's works"

(Gaffney, 1979: 105). In his influential textbook on phylogenetic systematics, Wiley (1981: 20) adopted "the hypothetico-deductive approach throughout", while Farris' (1983) evaluation of cladistic hypotheses of phylogenetic relationships in Popperian terms of 'degree of corroboration' and 'explanatory power' is still widely considered a classic.

Across the Atlantic, Günther (1956) praised Hennig (1950) for his 'empirio-critical' approach to systematics, and building on Hennig he presented phylogenetic analysis again in a hypothetico-deductive form (Günther, 1967). Schmitt (2001: 343) praised Hennig for having transformed systematics "from a skill or an art to a truly scientific method ... which justly takes its place in a hypothetico-deduc-

1. Department of Geology, The Field Museum, 1400 S. Lake Shore Drive, Chicago, Illinois 606605-2496. USA. E-mail: orieppel@fieldmuseum.org

tively structured science corresponding to the picture of science painted by Popper.” The first comprehensive textbook on phylogenetic systematics published in Germany again stipulated “a hypothetico-deductive method of scientific argumentation” (Ax, 1984: 59), and the same continues in more recently published German textbooks (Wiesemüller *et al.*, 2003).

Many more references could be added to the above bibliography that documents the tenacity with which phylogenetic systematists (cladists) defend(ed) a hypothetico-deductive form of argumentation for their science. In retrospect, this tenacity, which continues to the present day, seems rather surprising (e.g., compare Kluge [1983: vii], who at that time “remained unconvinced of the relevance and importance” of Popper’s hypothetico-deductivism for systematics with Kluge [2005]). Why surprising? Well, Hennig (1974) himself had remarked – in passing – that hypothetico-deductivism is not applicable to his method of phylogenetic analysis. Secondly, Sober (1988) elegantly demonstrated the inapplicability of Popper’s falsificationism to phylogenetic inference. Hull (1983) had previously already strongly discouraged the application of Popper’s ideas about science to systematics. And thirdly, philosophers registered a gradual demise of Popper’s philosophy of science in the 1960ies and 1970ies (e.g., Okasha, 2006: 72; Newton-Smith, 2001) already, i.e., at a time before cladists made him their patron saint (Hull, 1988). There had, indeed, been important philosophical criticism of Popper’s falsificationism (e.g., Kuhn, 1962, 1970, 1974; Putnam, 1974; Newton-Smith, 1981 [1994]; Worrall, 1989), which cladists chose to ignore. For example, Gaffney (1979: 80) cited Kuhn (1970) in support of his assessment that systematics was in “the first stages” of a scientific revolution, and while conceding that “the course of systematics [could be] more a problem in the sociology of science than the logic of science” (Gaffney, 1979: 79), he nevertheless turned to Popper in order to dress up systematics as a proper branch of modern science.

There have been several recent publications criticizing the application of Popperian falsificationism to cladistics (Rieppel, 2003, 2004, 2005; Rieppel *et al.*, 2006; Vogt, 2008). The arguments presented in these papers need not to be repeated here. In addition, Fitzhugh (1997, 2006a, 2006b, 2008) in a series of papers analyzed the formal structure of phylogenetic inference, arguing that it is neither deductive, nor inductive, but abductive instead. As explained below, deduction draws out the conclusion that is logically entailed in the premises: it is about what necessarily must be the case. Induction concludes from observa-

tion to a generalization: if all the swans I have ever seen were white, I might conclude that ‘all swans are white’. Inductive generalizations are not necessarily true, but only probable, and may be wrong, as when black swans are discovered in Australia. Abduction is a form of argument that seeks a causal explanation of the data: if in the morning a piece of cheese left on the kitchen table shows carvings of little rodent teeth, and there are small droppings on the floor, the most likely explanation of those observations is that there must be a mouse hidden somewhere. An abductive inference again is only probable and can be wrong: it could have been the hamster from the little girl next door that had escaped and made his home in the neighbor’s kitchen, but that explanation appears (intuitively in this example) less parsimonious (see Godfrey-Smith, 2003, for further discussion).

Fitzhugh (1997, 2006a, 2006b, 2008) used its abductive nature to justify both parsimony and the requirement for total evidence in phylogenetic inference. Abduction is also known as ‘inference to the best explanation’. Given a certain character distribution amongst terminal taxa, the most parsimonious phylogenetic hypothesis best explains the data (characters) as caused by descent with modification. The doctrine of total evidence requires taking into account all available evidence insofar as it has relevance to an inference. Fitzhugh takes the observation of characters as evidence, and finds its relevance to derive from the way this evidence supports, or contradicts, phylogenetic inference under parsimony. In summary, Fitzhugh (1997, 2006a, 2006b, 2008) evaluates the relevance of the evidence in terms of its congruence or incongruence relative to phylogenetic inference, and roots the causal explanation of the relevant evidence in descent, with modification (Mayr’s, 1982, ‘ultimate cause’).

Here, I propose to take a somewhat different approach to the analysis of the claim that cladistics is hypothetico-deductively structured and yet tied to the requirement for total evidence. Specifically, I want to contrast two classic models of scientific explanation, the deductive-nomological and the inductive statistical models to show that the total evidence requirement is automatically fulfilled in a hypothetico-deductively structured argument. In contrast, consideration of the total evidence is non-trivial for inductive or abductive reasoning, but again only as far as it is relevant for any inference. In contrast to Fitzhugh (1997, 2006a, 2006b, 2008), I propose to root the relevance of evidence in phylogenetic inference not only in congruence, but also and more fundamentally in theories of inheritance, development, and function (the ‘proximate causes’ of Mayr, 1982).

DISCUSSION

A Matter of Law

In his 'Logic of Scientific Discovery', first published in 1935, Popper (1959 [1992]) developed a certain form of 'covering law model of scientific explanation', which was later generalized and more stringently formalized by Hempel & Oppenheim (1948; also Hempel, 1965, 1966). Popper's basic idea was to start with the formulation of a law of nature. Popper did not consider it an important question how we get to the statement of a law of nature in the first place. For him, such laws were just stipulated ("invented" in Kuhnian terms: Kuhn, 1974: 2). The reason is that Popper thought we could never know any such law of nature to be true anyway. In contrast, he thought we could know them to be false: a law of nature, once formulated, could be found to be false. The reason is that a law of nature would allow the deduction of a sentence that would report on the exemplification of that law in nature. If that deduced sentence was found to be true, the law was not necessarily true also. But if the observation statement deduced from the law was found to be false, then the law from which it was deduced must be false also.

It is important to notice several, perhaps not readily apparent aspects of this Popperian train of thought. First of all: deduction is a logical relation. Logical relations hold only between sentences (and the propositions, or thoughts they express), not between sentences, or words, and things. If observation sentences can be deduced from laws, then laws must be sentences also. Laws are not in nature. Natural laws cannot be picked up and kicked away. Laws are something we say about nature: laws say that nature is so-and-so, and what laws say may be right or wrong. Nature cannot be right or wrong, it just is.

Similarly then, observation statements (reports, sentences) deduced from such laws are likewise something we say about nature, and again, what they say may be true or false. Popper's first claim to fame was his insight that there is no theory-free observation. If that is true, there is no theory-independent way of knowing whether an observation statement is true or false. This particular issue has been subject of much discussion, but will not be treated in detail here. Suffice it to say that Popper (1974a) compared the scientific community to a jury in a court of law, and he left it up to those jurors and their deliberations to decide whether a particular observation report was true or false, or whether it should be provisionally accepted to be true or false pending further testing.

The other, and in the present context more important issue, is that these observation statements, which are to describe an exemplification of a law in natural events or processes, is itself deduced from that law. That is how observation statements can test the law from which they are deduced. If the observation obtains, if the scientific jury decides that the observation report is true, then that report coheres with the law from which it was deduced. In that circumstance, Popper saw the law as corroborated. If the natural state of affairs described by the observation statement does not obtain, if therefore the scientific jury decides that the observation statement is false, then the observation statement logically contradicts the law from which it was deduced. The logical law of non-contradiction says that of two contradictory propositions, P & $not-P$, only one can be true; one must necessarily be false. So if the scientific jury decides that an observation statement is (to be taken to be) true, and if that observation statement contradicts the law from which it was deduced, then that law must be false.

However, and importantly: the deduction of an observation statement requires that the law, i.e., what we say about nature, be said in a particular way. And it is also precisely this particular way in which we must formulate a law that renders it impossible to know such a law to be true, whereas it can be known to be false. In order to allow the deduction of observation statements, the law must be formulated as a *universal statement*. Accordingly, Popper *defined* scientific theories as a set of sentences that must include (at least one) universal statement (Stamos, 2007). To be testable, a scientific theory, according to Popper, must make reference to a universal law of nature.

Such a universal law (theory) of nature is a very strong statement about nature. It states that nature could not possibly be otherwise than described by that law, if the law is true. Universal laws impart *necessity* on the natural processes or events that are explained by such laws. A natural event, or a natural process, that is governed by a universal natural law, must necessarily obtain in an identical way in all possible worlds imaginable. There could not be a world imaginable in which such an event, or process, could fail to obtain, or would obtain differently, given the relevant conditions for it to obtain at all. There could not be a world imaginable in which such a universal law could be suspended. This is what makes deduction from universal laws possible in the first place, and it is also the reason why universal laws can never be known to be true.

If an observation statement stands in a logical contradiction to the law from which it was deduced,

and if that observation statement is judged to be true, then the law is falsified. In contrast, if we want to know whether a universal law of nature is true, we would have to test it, and find it corroborated (confirmed), under all imaginable circumstances. But since there is an infinity of imaginable worlds, it would take an infinite number of tests with positive outcome to prove such a law to be true. Since that can never be achieved – not just as a matter of practicality, but as a matter of principle – we can never know such a universal law to be true.

It should now have become apparent that there cannot be any universal law of nature that governs the evolutionary process, as Popper (1974b) indeed recognized when he called evolutionary theory a ‘metaphysical research program’. Take character congruence for example. Many logicians are suspicious of definitions, since definitions are arbitrary, or at least conventional. They prefer to fix the meaning of a term extensionally: the meaning of a term is given by all the objects in the world ‘out there’ to which the term truthfully applies. The meaning of ‘chordates’, for example, is given by the totality of all organisms that have a notochord (rather than by a definition). The law ‘*all* chordates are renates’, being a universal law, thus states that, *necessarily*, all organisms that have a notochord also have kidneys. According to this law, there could be no world imaginable in which organisms existed that have a notochord but no kidneys, or *vice versa*. But evolution is not a process governed by necessity. Instead, it is a historically contingent process. Perhaps there are historical, or physiological reasons that render the existence of a chordate without kidneys unlikely. But it is not impossible to imagine a chordate without kidneys. There is no logical contradiction in the statement ‘there exists a chordate without kidneys’. ‘*All* tetrapods have lungs’ is a statement in the form of a universal law. But we know that lungless frogs, and salamanders exist. This is what Sober (1988) meant when he said that there is no deductive link between a phylogenetic tree (hypothesis) and the character distribution on that tree. There is no universal law of evolution that governs character distribution. Character distribution is historically contingent, and the evidence for that fact is character incongruence.

The Deductive-Nomological Model of Scientific Explanation

Why do we need universal laws (i.e., *All* – statements) in hypothetico-deductivism? The reason is

the deductive component of the argument. Deduction is truth preserving: if it is true that all humans are mortal, and if it is true that Socrates is human, then it is necessarily also true that Socrates is mortal. If the premises are true, there cannot be any world imaginable in which Socrates would not be mortal. It is impossible to say that Socrates is mortal today, but might become immortal tomorrow. For what is true today cannot be found false tomorrow. What is found false tomorrow must be erroneous today.

Now, a scientist might ask the question: “Why is Socrates mortal?” This question specifies the state of affairs that the scientist seeks to explain. This is called the *explanandum* in a deductive-nomological argument. The answer is: “All humans are mortal” and (&X) “Socrates is human.” ‘All humans are mortal’ is the statement of a universal law of nature. ‘Socrates is human’ is called an initial condition. It states that there exists a thing called Socrates, and that this thing is a human being. Combining (logically: conjoining) the law statement (*L*) ‘All humans are mortal’ with the initial condition (*i*) ‘Socrates is human’ *explains* (is the explanans for the explanandum) why Socrates is mortal. The reason is that the conclusion can be *deduced* from the premises. Given the Law (*L*), and the initial condition (*i*), the explanans (i.e., ‘All humans are mortal’ & ‘Socrates is human’) deductively (logically) entails the explanandum (i.e., ‘Socrates is mortal’). The Deductive-Nomological (D-N) model of scientific explanation (Hempel & Oppenheim, 1948; Hempel, 1965, 1966) provides necessary and sufficient conditions for an explanation. If the premises (explanans) deductively entail the conclusion (explanandum), nothing more is needed for a successful explanation: the explanation is said to be complete. But in order to deductively entail the explanandum, the explanans (the premises) must include (at least one) statement of a universal law. If phylogenetic systematics cannot afford a universal law of nature, it cannot be structured as a D-N model of explanation.

A scientific explanation along the lines of the D-N model, if valid and sound, is complete. In contrast, systematists say that phylogeny reconstruction is never complete. There is always the possibility – in practice, not in principle – to add more characters, and more taxa, to an analysis. From there, cladistics appeals to the principle of total evidence (Kluge, 1989). But total evidence is not a requirement linked to the D-N model of explanation. As long as the explanans (the premises) deductively entails the explanandum (the conclusion), the explanation is complete. The requirement of total evidence is automatically fulfilled in the D-N model of scientific explanation (Salmon,

1998; *pace* Kluge, 2004). Consider the effect of adding initial conditions (*i*) to the example above:

- (*L*) ‘All humans are mortal’
- (*i*₁) ‘Socrates is human’
- (*i*₂) ‘Socrates is a man’
- (*i*₃) ‘Socrates’ wife is called Xanthippe’
- (*i*₄) ‘Socrates has a long beard’
- (*i*₅) ‘Socrates despises jewelry’
- etc. ...

Conclusion: ‘Socrates is mortal’

It is easy to see that the statement of the law (*L*) and the first initial condition (*i*₁) are both necessary and sufficient to arrive at the conclusion. All other premises (initial conditions *i*₂-*i*₅) are *irrelevant* to the explanation as to why Socrates is mortal. The requirement of total evidence is automatically fulfilled by (*L*) and (*i*₁).

‘Total Evidence’ versus ‘Relevant Evidence’

If phylogenetic (cladistic) inference is hypothetico-deductively structured in the sense of the D-N model of scientific explanation¹, then there is no requirement for total evidence. If there is a requirement for total evidence in phylogenetic (cladistic) inference, then that mode of inference is not deductive-nomologically structured. Since cladists *do* appeal to the requirement of total evidence, cladistic inference is inductively, or abductively structured (Fitzhugh, 1997, 2006a, 2006b, 2008). Indeed, the principle of total evidence has originally been invoked in the con-

text of inductive inference (Carnap, 1950; Hempel, 1962).

Various models of inductive inference have been developed over time, which cannot all be mentioned here (e.g., see Salmon, 1998). The inductive counterpart to the D-N model is the Inductive-Statistical (I-S) model of scientific explanation (Hempel & Oppenheim, 1948; Hempel, 1965, 1966). It again starts from a set of premises, which constitutes the explanans that explains the explanandum. However, in this case, the explanandum is not logically (deductively) entailed by the explanans. That is to say, the explanandum (the state of affairs to be explained) does not obtain necessarily if the conditions obtain that are described by the premises. Instead, the explanandum will be expected to obtain with some probability only given the premises². And evidently, the more evidence that goes into the premises, the higher will the probability be for the explanandum to obtain. From this follows the requirement for total evidence. But Salmon (1998: 364; as also Hempel, 1977) rejected the requirement of a high probability for statistical explanation, and requested a “relevance requirement” for the evidence instead.

A distinction must therefore be drawn between the total evidence, and the total relevant evidence. This can be nicely brought out with a paradox of confirmation (e.g., Hempel, 1965). Suppose it is a universal law that ‘all ravens are black’ (technically: ‘for all *x*, if *x* is a raven, *x* is black’). If that is true, then it must also be true – on grounds of logical equivalence – that ‘anything that is not black is not a raven’ (technically: ‘for all *x*, if *x* is not black, *x* is not a raven’). On grounds of logical equivalence one can also transform the first statement into a third one: if something

1. The deductive-nomological model of scientific explanation entails a very strong notion of explanation that appeals to logicians, but perhaps not so much to empirical scientists. Indeed, there is good reason to claim that the D-N model is too strong for empirical sciences: “many scientific explanations ... either do not contain exceptionless laws or do not strictly entail the phenomena” (Lipton, 2004: 26). In view of such problems, one might operate with scope restriction for laws. ‘All fishes are infected by XYZ’ is a universal law of unrestricted scope that cannot be verified; ‘all fishes in the pond in my back yard are infected by XYZ’ is an ‘all-statement’ of restricted scope, for which reason it can be verified, and something can be done about the disease. The problem only is that scope restriction can be practiced to a degree that renders the problem to be explained, and its explanation, uninteresting (Kitcher, 1993). Cladists have restricted the scope of their hypothetico-deductive argument to the finite universe of a three-taxon statement (e.g., Kluge, 2003). Whereas a hypothetico-deductive argument scheme can be applied to the logic of a three-taxon statement (Ball, 1982), it is still too strong for cladistic purposes. To say that Socrates is mortal because he is human & all humans are mortal, is to say something general about Socrates and all other humans. Nothing is said about when, where, and how Socrates will eventually die. But Socrates will eventually die at some point in space and time and under some circumstances, which means that the law ‘all humans are mortal’ materially implies that Socrates will eventually be dead if he is human. It is this relation of material implication that spoils the hypothetico-deductive reasoning applied to a three-taxon statement (see Rieppel *et al.*, 2006, for a detailed discussion). Ball (1982) thought that hypothetico-deductivism could apply to a three-taxon statement, but because he recognized the strength of the relation of material implication, he had to base this positive conclusion on the fact that we can *unfallibly* recognize which character statements (i.e., observation statements in systematics) are *true* homologies, and which ones are *true* homoplasies. We know that this is impossible in practice, as it is also impossible in principle, because all observation is theory-laden.

2. There have been attempts to develop a version of the D-N model of explanation that could handle inherently indeterministic (probabilistic) processes such as radioactive decay. However, these models are tied to Popper’s famous propensity interpretation of probability, which is “notoriously unclear” (Railton, 1978: 222; for further discussion see Rieppel, 2003).

is either a raven, or not a raven, then that thing is either not a raven, or it is black (technically: for all x , if either x is a raven or x is not a raven, then either x is not a raven or x is black'). Given these logical permutations of the statement 'all ravens are black', and maintaining the principle of logical equivalence as valid, the conclusion is that any observation of anything that is not black – white tennis shoes, green leaves, or blue whales – confirms the statement that all ravens are black (for further discussion see Ayer, 1972 [2006]). White tennis shoes, green leaves and blue whales could thus be part of the 'total evidence' that confirms the statement 'all ravens are black'.

Logicians have discussed and exploited that paradox in many different ways, but for biologists this whole exercise may seem a bit pointless. Surely there is a counterintuitive conclusion here that is rooted in logic, but for a biologist, white tennis shoes, green leaves, or blue whales are simply irrelevant to the question of whether or not it is true that 'all ravens are black' (see also Lipton, 2004; Salmon, 1998). So here again it becomes obvious that the relevant evidence has to be distinguished from the total potentially available evidence as one proceeds to ponder whether it is true that all ravens are black. We know that the reliable observation of a white raven would render the statement false, but that is not the question. The question is whether a statement such as 'all ravens are black' can be found to be true, or – if we join Popper in saying that this question has no answer – whether such a statement can be accepted as one with a high probability.

Cladists of the Popperian brand will point out that this whole discussion is misguided, or at least has no relevance to their research program, for they are not interested in the confirmation of a cladogram. All that counts is the evaluation of alternative cladograms in terms of relative degrees of falsification, and complementarily, relative degrees of corroboration (e.g., Kluge, 1997a, 1997b). This argument gains little purchase, however, as it leads either to extreme skepticism, or to closet inductivism. If cladograms are evaluated in terms of relative degrees of falsification (e.g., Grant & Kluge, 2007), all one does is evaluating alternative hypotheses of relationships with respect to their falsity content. There is no positive knowledge, nothing can be known to be true, everything can only be known to be (more or less) false. The result is an extreme skepticism. However, Popper linked 'degree of falsification' with 'degree of corroboration'. Popper (1979) developed the idea that whereas Newton's theory is highly corroborated, Einstein's theory earns an even higher degree of corroboration because it an-

swers all the questions Newton's theory answers and even more. This idea Popper (1963) developed into his concept of verisimilitude that measures the relative truth content of alternative theories as opposed to their relative falsity content. Popper's concept of 'verisimilitude' was doomed to failure (Miller, 1974; Tichy, 1974), but one aspect – its link to 'degree of corroboration' – remains worth exploring. Remember that Popper denied all possibility of inductive inference; he also denied that any scientific theory (defined as a universal statement) could ever be known to be true – it can only be known to be false. From these results Popper's extreme skepticism. A Popperian standing on the top of the Eiffel Tower has no positive argument why he should take the stairs down rather than jump off the tower in the expectation to gently glide to the ground (Worrall, 1989; see also Putnam, 1974). To claim that Galilei's laws are highly corroborated, and that to take the stairs would therefore be a safer way down, makes an inference from the past performance of Galilei's laws to their future performance. This is Popper's closet inductivism. Popper (1974a: 1193, n.165b) admitted to "a 'whiff' of inductivism" in his reasoning, which "enters ... with the assumption that science can progress towards greater verisimilitude". "On one meaning of the word 'whiff' a whiff is 'a kind of fish', and certainly this kind of argument is fishy. On another construal 'whiff' is a puff of air. But it is just false to say that there is a whiff of inductivism here – there is a full-blown storm" (Newton-Smith, 1981 [1994: 68]). This shows that unless one adopts Popper's extreme skepticism, his notion of 'corroboration' is hardly different "from what the inductivists mean when they say that a hypothesis has been confirmed" (Ayer, 1972 [2006: 74]).

Relevant Evidence in Systematics

Cladists by and large agree that Hennig's (1950) criterion of monophyly marks out *natural* groups. The goal of cladistics is therefore a natural system (classification) of monophyletic clades (groups). According to Hempel (1965: 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." Hempel's criterion of naturalness translates into character congruence in cladistic analysis. The 'coming together' of (independent) characters in support of a hierarchy is what licenses the evolutionary

explanation of that hierarchy. Hempel (1965: 352) based such ‘coming together’ of evidence on the “*laws of coexistence*”, as opposed to the “*laws of succession*”, thus embracing a “silence about causation” (Rosenberg, 2005: 32). The cause precedes its effect. Hume’s minimalist account reduced causation, i.e., the relation of cause to effect, to temporal precedence, spatiotemporal contiguity, and constant conjunction. Hempel’s ‘law of coexistence’ is even more minimalist, and hence abandons the need for causal relations in scientific explanations: “In particular, there is no requirement by Hempel that the premises must tell us anything about the cause of the event to be explained. Hempel is particularly insistent on this point” (Ruben, 1993: 4). An effect follows a cause, but in contrast to Hempel’s ‘law of succession’, his ‘law of coexistence’ has no temporal dimension. This opens the door to an instrumentalist perspective in systematics (Rieppel, 2007).

A scientific realist argues that scientific theories are approximately relevantly true, i.e., approximate the world as it really is, outside of mind and discourse. Airplanes don’t crash because our laws of aerodynamics are approximately relevantly true. And should an airplane crash, the cause of the accident can be investigated, and many times identified. Instrumentalists argue that scientific theories do not make such ontological commitments to the world, or if they do, that this is an excess content that the theory can shed without harm. For an instrumentalist, a scientific theory is not approximately relevantly true, but empirically adequate (van Fraassen, 1980). Its empirical adequacy is measured by its predictive power. But as Hennig (1974) realized already, predictiveness is not a property that characterizes systematic theories, certainly not in terms of the D-N model (its premises including a universal law), nor in terms of the I-S model (its premises including a statistical law) of scientific explanation. Accordingly, cladists evaluate hypotheses of phylogenetic relationships not in terms of their predictiveness, but in terms of their explanatory power: the ‘coming together’ of characters, i.e., character congruence, is explained in terms of homology, i.e., common descent. Cladistic analysis organizes data, whatever these are, in an optimal way relative to some optimality criterion, such as parsimony, and then proceeds to dress up the resulting tree as an estimate of phylogenetic relationships: the “most parsimonious

trees are trees on which the greatest amount of putative homology statements ... *can* be explained as due to inheritance and common descent, and such trees are the best available phylogenetic hypotheses for the terminals at hand, whether or not the individual similarity statements or their explanations are historically correct” (De Leat, 2005, p. 88).

But what does it mean to characterize the correctness of the historical explanation of character statements as irrelevant? Bertrand & Härlin (2008: 339) characterize the realist claim of a growing correspondence of phylogenetic hypotheses to “the real phylogeny” as an “admirable but nevertheless a very idealistic picture of taxonomy.” They go on to assert that “while phylogeny is an evolutionary process, taxonomy is a human activity ... our reconstructions and representations have a profound influence on how we talk and think about the true phylogeny” (Bertrand & Härlin, 2008: 340). Human thought and discourse thus reconstructs and represents – at least in part – the scientific reality of the taxonomist³. And indeed, if there is no theory-free observation, character statements are low-level hypotheses, which have to be evaluated by the scientific community engaged in systematics. What does it mean, then, to say that “no special procedure is required for [character] hypothesis ‘generation’” (Wheeler *et al.*, 2006: 10)? How is it possible, on that basis, to distinguish total evidence from relevant evidence, if such a distinction is required for sound inductive (abductive) inference? In his discussion of the requirement of total evidence, Salmon (1998: 340) recognized that requirement as a way to ensure that the inductive inference will be a strong one, yet qualified total evidence as a requirement for all *relevant* evidence, i.e., evidence “*of an appropriate sort*” (Salmon, 1998: 305).

The mere ‘coming together’ of character statements is not enough to demonstrate their relevance (Lecointre & Deleporte, 2005). The mere congruence of characters is too weak to show that the characters are ‘of an appropriate sort’, especially not if the ‘correctness’ of ‘individual similarity statements’ is considered irrelevant (De Leat, 2005), or a method for the generation of character statements is denied (Wheeler *et al.*, 2006). Similarity, it is often said, is in the eye of the beholder. Indeed: pigs and oysters share a similarity, i.e., they are not eaten by orthodox Jews (Sterelny & Griffiths, 1999). Should this similar-

3. Consider the traditional notion of a ‘*natural kind*’ as a sample of stuff, or a collection (or aggregate) of things that *occur in nature* and that, in virtue of shared causal dispositions, exhibit lawful behavior at least to some degree (e.g., Griffiths, 1999). Bertrand and Härlin (2008: 343) contrast this traditional conception of natural kinds with their own version of natural kinds as “sets of phylogenetic hypotheses.” This must mean that phylogenetic hypotheses – *qua* tokens of a natural kind – constitute the taxonomist’s reality.

ity even be considered as a potential homology of pigs and oysters, or should such a character statement be rejected outright? Evidently, it could be conjectured as a possible homology statement, but it won't stand the test of congruence. So there is no way around the fact that the test of congruence is a necessary condition for cladistic analysis (Fitzhugh, 2006a, 2006b; Kearney & Riepel, 2006). But it is not also a condition sufficient for the distinction of relevant evidence from all total evidence potentially available. What in addition is required is a causal grounding of character statements in theories of inheritance, development, and function.

Causal relations imply reality: it is hard to imagine things that do not exist to enter into causal relations. The 'law of coexistence' may remain silent about causality, character analysis cannot. To be relevant for phylogenetic analysis, character statements have to convey information relevant to that project, information of the right sort for that project. Character statements gain that information content through their causal grounding in theories of inheritance, development, and function. Such causal grounding may be direct, as through the investigation of the developmental mechanisms at work in a tetrapod limb bud, or indirect through the application of criteria of topology and connectivity that are themselves grounded in ontogeny. According to Platnick (1982: 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." This is evidently wrong: the character 'spinnerets' is causally grounded through its function – it's a spider's silk-spinning organ. This organ is located in the abdomen, which is identified through its topology and connectivity as determined by the embryonic development of the spider, etc.

The same argument applies to molecular data. Their causal grounding requires to take into account what is known of DNA function and sequence evolution, even if such knowledge still remains relatively limited, yet is complex (e.g., Philippe *et al.*, 2005). Vertebrate paleontologists are not willing to disregard all the evidence provided by fossils for the origin of mammals in order to maintain putative homologies that render mammals the sister-group of birds. The fossil record, and its interpretation from a morphological, developmental, and functional perspective, played an enormous role in segregating relevant from irrelevant evidence for the sister-group relationships of mammals (e.g., Kemp, 1983; Gauthier *et al.*, 1988; Kirsch & Mayer, 1998). A sister-group relationship of birds and mammals was postulated both

on morphological (Gardiner, 1992, 1993) and molecular (Hedges *et al.*, 1990) grounds. The inclusion of fossils in the analysis reverted those relationships and recovered the traditional Archosauria again, with birds being the sister-group of crocodiles amongst extant amniotes (Gauthier *et al.*, 1988). Kemp (1988) optimized characters on the ancestral node of birds and mammals showing that the putative ancestor of Haemothermia would not have been a viable organism. Since endothermy was used as a putative synapomorphy of birds and mammals (Gardiner, 1982), their most recent common ancestor would have to have been endothermic. And yet, this organism could not have had body insulation, since hair and feathers have radically divergent ontogenetic trajectories and therefore are considered to be non-homologous. Why should molecular systematists disregard concern for the complexities of life? Nucleotides per se may lack the structural or developmental complexity that are exhibited by morphological systems (Frost *et al.*, 2006: 14), but that does not speak to the complexity of DNA function and sequence evolution. Proponents of direct optimization techniques (Wheeler *et al.*, 2006) need to be concerned about the optimization of DNA sequence data to ancestral nodes, and their biological relevance for such an ancestral condition.

CONCLUSIONS

A review of covering law models of scientific explanation (Popper's falsificationism and the Hempel-Oppenheim deductive-nomological model) shows that phylogenetic systematics (the cladistic analysis of phylogenetic relationships) is not hypothetico-deductively structured. If it were, there would be no reason to call for total evidence, since that requirement is automatically satisfied in a deductively structured explanation, where the explanans logically entails the explanandum. In fact, the appeal to the requirement of total evidence (Kluge, 1989, 2004) indicates that phylogenetic inference based on the principles of cladistic analysis is inductively, or abductively, structured (Fitzhugh, 1997, 2006a, 2006b, 2008). The principle of total evidence has been invoked to render inductive inference an argument as strong as it can be, but for this to be the case the total evidence must also be relevant evidence, i.e., evidence of the right sort (Salmon, 1998). Character congruence is a necessary condition for phylogenetic inference, but not also a sufficient condition. What is required in addition is the causal grounding of character state-

ments in theories of inheritance, development and function. Homology is a relation; homologues are parts of organisms entering into this relation. To call parts of organisms homologous means to reify (i.e., to turn a concept into a thing) the relation of homology. The way to do so is through causal grounding (Rieppel & Kearney, 2007): causal relations are existence implying.

It is often said that such causal grounding can go wrong: why should ontogeny provide causal grounding for character statements, when ontogeny itself can change and evolve? Enough examples are known of putatively homologous features that share different ontogenetic trajectories, or putatively non-homologous features which share a similar ontogenetic trajectory (Hall, 1995). True enough – but the trick here is not to set the bar of knowledge impossibly high. That scientists are prone to make mistakes is no reason to reject theories of inheritance, development, and function in character analysis. Once hypothetico-deductivism is left behind, certainty and necessity are no longer issues in scientific reasoning. Their place is taken by probability.

RESUMO

A sistemática filogenética (ou análise cladística das relações filogenéticas) não é estruturada de uma maneira hipotético-dedutiva (no sentido de um modelo de lei de explanação científica abrangente). Se esta fosse, não haveria razão de apelar para o princípio de evidência total, já que este requisito encontra-se automaticamente preenchido em uma explanação estruturada de forma dedutiva. Alternativamente, a demanda pelo requisito de evidência total na sistemática filogenética indica que a inferência filogenética é estruturada de forma indutiva ou até mesmo abdutiva. O princípio de evidência total foi invocado no sentido de transformar a inferência indutiva em sistemática em um argumento tão forte quanto possível, mas para que isto ocorra o princípio de evidência total deve representar também evidência relevante, isto é evidência “do tipo certo” em relação ao assunto a ser esclarecido. A congruência de caracteres constitui-se em uma condição necessária à inferência filogenética, mas não deve ser vista como uma condição suficiente para esta última. O que parece faltar é uma base causal na definição de caracteres em teorias de herdabilidade, desenvolvimento e função.

PALAVRAS-CHAVE: Hempel, Popper, cladística, hipotético-dedutivismo, evidência total, evidência relevante.

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