
CAN A CLADOGRAM BE FALSIFIED?

CAMILO J. CELA-CONDE

ABSTRACT. A bottom-up way is a means of reaching knowledge, starting at the bottom level of raw data, and arriving at the top level of a more general description. Several authors—such as Delson, Eldredge and Tattersall (1977), Skelton, McHenry and Drawhorn (1986), and Strait, Grine and Moniz (1997)—attempt to use bottom-up methodologies in the paleontological field. However, if problems like those of trait biases must be avoided, it seems difficult to disregard functional criteria when constructing cladograms. Since functional criteria works on a top-down way—starting at a higher level of knowledge we deduce a lower conclusion—the naïve aim of constructing phylogenies in an extreme bottom-up way ends up by being hard to reach.

KEY WORDS. Cladogram, falsification, phylogeny, bottom-up knowledge, hypodigm, parsimony scenario, phylogeny, species, ancestor-descendant relationship.

This paper refers to the question of whether a cladogram can either be falsified or not. Please allow me, in the first instance, to clarify what I mean by “be falsified” and “cladogram.”

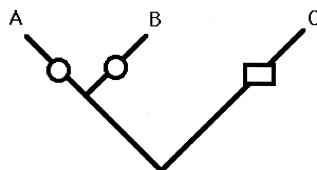
As is widely known, Popper’s principle of falsifiability is an epistemological tool to decide whether a theory, or a hypothesis, is actually false or must be considered (provisionally) true. When proposing the falsification criterion, Popper had in mind a definite meaning of “theory”—such as the Newtonian and the Einsteinian theories. In fact, Popper explicitly rejected biological taxa as the proper subject for his principle of falsifiability. However, some scholars working in different areas of the Life Sciences, such as Wiley (1975), Engelman and Wiley (1977), Platnick and Nelson (1978), Cracraft (1981), Cartmill (1981), Hull (1983), Rieppel (1997) or Kluge (1997), have made use of what we may call the “Popperian spirit of falsifiability” (Settle, 1979) to test taxonomic or systematic hypotheses.

By “cladogram,” we may use Wiley’s (1981, p. 97) notion: “A branching diagram of entities where the branching is based on the inferred historical connections between the entities as evidenced by synapomorphies.”

Cladograms are normally built from morphological sets of characters, but this is not a logical prerequisite. Behavioral traits and molecular data sets may be also considered sources for a cladistic study. Sanderson and Donoghue (1989) and De Queiroz and Wimberger (1993) compared the level of homoplasy respectively in molecular/morphological sets and behavioral/morphological sets, showing that neither of them is useful for estimating a phylogeny. However, when we deal with data coming from the fossil record, morphological characters are the main items of evidence. Consequently, I will refer only to morphological characters from now on.

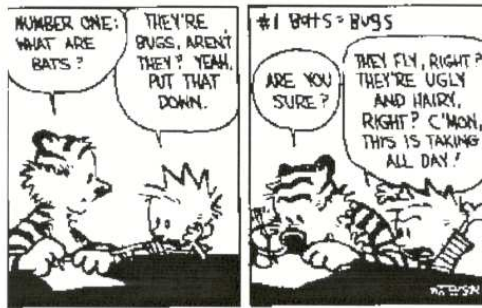
On the bases of these two definitions, a cladogram can be falsified, in principle, if we show just one counter-instance. Since the historical connections of cladistic branching is evidenced by synapomorphies, an example of an ill-founded synapomorphy would suffice, i.e., a character that is actually a homoplasy, but we mistake it for a homology. However, philosophers of science, like Sober, disagree in their consideration of how synapomorphies and homoplasies may be identified. As Sober says: "It is important to bear in mind that cladograms themselves do not imply that any synapomorphy is a homology; to say that an apomorphy is unique to a particular monophyletic group leaves open whether it evolved once or many times" (1983, p. 340).

Sober's warning is irrefutable. In the following diagram, taxa A and B may have a shared character (the round character) either because it was present in a common ancestor (a plesiomorphy) or because it evolved several times in the monophyletic group. The absence of the character in C does not, in itself, resolve the ambiguity. Perhaps the character disappeared in lineage C.

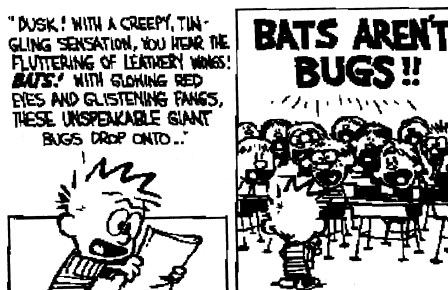


In the absence of any other kind of information, any character can always be interpreted as a homoplasy. Fortunately, we can distinguish between homologies and homoplasies by taking into account the general process of evolution. However, most statements that we could make at this level are truisms nobody will disagree with; circularity appears in these cases. To identify homoplasies we need a description of the general process of evolution, in order to be able to check out whether common ancestors have, or have not, the suspected analogous character. But to have a description of the evolutionary process is equal as having the cladogram

we are trying to falsify. Only massive taxonomic errors may be identified in this way. Let me give an example.

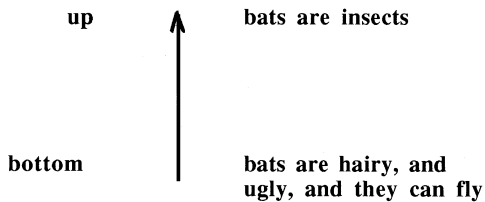


As a taxonomist, Calvin makes an assumption based on several traits. Bats are bugs because they can fly, and because they are ugly and hairy. To fly, and to be ugly and hairy are shared characters, synapomorphies between bats and bugs, if we are allowed to translate Calvin's assumption into the jargon of systematics. However, not everybody agrees with this. When Calvin read his report, schoolkids unanimously disagreed:



Both bugs and bats can fly, and both are hairy and ugly, but those are just analogous characters. As Calvin's schoolkids, we are well aware of the evolutionary journey of mammals to disregard these kind of homologies shared by bugs and bats. Epistemologically speaking, Calvin follows a "bottom-up" way.

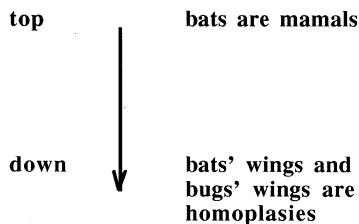
Calvin's epistemological scheme:



A bottom-up way is a means of reaching knowledge, starting at the bottom level of raw data, and arriving at the top level of a more general description. If we check bats out, and observe that they fly, and they are hairy and ugly, we are not making any taxonomic assumption about them at the moment—we are just describing some raw characters that they both have. Taxonomic proposals come later, as a result of the bottom-up approach.

Calvin's schoolkids, on the other hand, follow a top-down route. Starting at a higher level of knowledge—they *know* that bats are mammals—they deduce a lower conclusion—thus, bats' wings and bugs' wings are homoplasies.

The schoolkid's epistemological scheme:



The bottom-up/top-down distinction has been an important methodological tool to understand knowledge processes. For instance, the philosopher Jerry Fodor (1983) gave a model of the human mind that distinguishes between perception and cognition. Perception is modular and proceeds in a bottom-up way, while cognition is holistic and proceeds in a top-down way. However, neurologists, like Ramachandran, proved that cognition could invade low levels of perception in a top-down way, as in the blind spot phenomenon. The human brain transforms the blind spots not by ignoring them, but by filling them in by means of an active knowledge task (Churchland and Ramachandran, 1993). Any task of knowledge normally implies both the bottom-up and the top-down proc-

esses in a feedback scheme. General assumptions lead to some particular interpretations of new data, new data may change our general assumptions, and so forth. Anyhow, what we should now try to clarify is what kind of process is more appropriate in the field of systematics.

If we follow a top-down way, to falsify a general taxonomic hypothesis is a trivial and easy task, since circular arguments are obvious in themselves. If bats belong to the mammal class, they are not insects, so we can shout out at Calvin that bats aren't bugs. The same applies when we try to classify the human lineage. Vervet monkeys, for instance, have oral semantic communication at quite a high level (Cheney and Seyfarth, 1992), but they belong, in no way, to the *Homo sapiens* taxon.

However, a different question arises when we cannot identify homoplasies, because the right evolutionary episode is missing. For instance, if we try to falsify the assumption: "*Paranthropus robustus* and *Paranthropus boisei* form a monophyletic group," we cannot refer to a well-known phylogeny to infer whether the robust masticatory apparatus is either a homoplasy or a synapomorphy. In fact, this phylogeny is what we actually try to establish.

In this case, what we will find are different cladograms that lead to different phylogenetic interpretations of an evolutionary episode. Thus, the question of falsification means, now, that we could choose between opposite cladograms, labeling one as "false," and provisionally accepting the other. How this task may be carried out is a controversial subject. In search for an accurate way to establish definite phylogenetic relationships between taxa, some authors rule top-down procedures out. For instance, Delson, Tattersall and Eldredge (1977) say:

The simple truth is that the sundry hominid 'phylogenies' available in the literature are scenarios—amalgams of statements of ancestor-descendant relationship thoroughly admixed with, and largely (although not always consciously) based on, *a priori* models of the evolutionary process, on interpretations about the significance of the stratigraphic and geographic occurrence of fossils, and reconstructions of paleoenvironment and functional anatomy, hence adaptations of these creatures. Statements as complex as these, as far removed from the data base as they frequently are, are difficult to test rigorously and leave us only with a vague feeling that one seems more 'sensible' or more plausible probabilistically than another (p. 263).

Delson, Eldredge and Tattersall (1977), Skelton, McHenry and Drawhorn (1986), and Strait, Grine and Moniz (1997) are examples of such attempt to use bottom-up methodologies in the paleontological field. According to Skelton and collaborators (1986) phylogenetic analysis must proceed by a series of logical steps:

- (i) Establishing a morphocline.
- (ii) Determining the direction of change in the morphocline.
- (iii) Constructing a cladogram.
- (iv) Deriving a phylogeny.
- (v) Postulating a scenario.

This series form a logical/temporal sequence—establishing a morphocline is the first step, at the raw-data bottom level, and postulating a scenario, the last one of them, at the highest level of knowledge. At step (iii) we could falsify two cladograms using, for instance, a parsimony criterion to decide which one of them better reflects the actual episode of speciation. As we all know, parsimony refers to the aim of minimizing the number of homoplasies and reversals of characters. Other criteria, such as cliques, or statistical methods among populations, can be used, yet parsimony is, traditionally, the most frequently used system to falsify. However, Maximum Likelihood Estimation (MLE) is growing in acceptance these days (see Huelsenbeck and Rannala, 1997; Pagel, 1999. For a criticism of the usefulness of MLE see Siddall and Kluge, 1997). The MLE of phylogeny is the tree for which the observed set of data is most probable. Therefore, since MLE seeks the most probable explanation of observed data, not the solution with the fewest events, the results of parsimony and MLE may be at odds with each other (Pagel, 1999). Nevertheless, this is not a huge problem. What we could take into account is that, by means of either parsimony or MLE criteria, it is possible to falsify a cladogram in a bottom-up way. Or, is it?

An example of a very accurate attempt to reach the human evolutionary episode by means of a bottom-up strategy is that of Strait, Grine and Moniz (1997) in their reappraisal of early hominid phylogeny. They proceeded in this way:

- (I) They chose nine species taxa, from *A. afarensis* to *H. sapiens*.
- (II) In each of the taxa, they included the specimens that will form the hypodigm.
- (III) They analyzed the characters of each of the hypodigms.
- (IV) They carried out eight parsimony analyses with PAUP 3.0s, to choose the best cladogram.

Is this a true bottom-up procedure? Three problems, at least, stop us from giving a straight “yes”. These three problems are:

- 1. Assigning characters to hypodigms.
- 2. Choosing species.
- 3. Assigning specimens to species.

Let me give an example of the first kind. Character number 20 of the list examined by the authors is a qualitative one—to have or to have not a sagittal crest, at least in presumpt males. Strait *et al.*, (1997, table 2) assign

this character to *H. habilis* and *A. africanus*—a conclusion that will certainly lead to some cladistic and taxonomic consequences.

Why did Strait *et al.* (1997) do so? In the Appendix 1, under the description of characters, the authors say: “A sagittal crest is present in KNM-ER 1805 and Stw 505 (Clarke, pers. comm.). Consequently, a sagittal crest is present in all hominid species except *H. rudolfensis*, *H. ergaster* and *H. sapiens*.”

The criterion used by the authors in order to assign a character to a species is as follows: “With respect to qualitative characters (...) a fossil species was here characterized as exhibiting a particular morphology only if it was present in every relevant specimen in the hypodigm” (Strait *et al.*, 1997, p. 30). Furthermore, any character that is known to be highly sexually dimorphic was restricted to a consideration of the morphology of only one sex. In the case of sagittal crest, this character should have been assigned to *A. africanus* and *H. habilis* if, and only if, it was present in every relevant specimen in the hypodigm. As many as 18 crania belong to the hypodigm of *A. africanus*, and 13 crania to *H. habilis*. Does this mean that all other specimen, except KNM-ER 1805 and Stw 505, were females, or that they were not relevant?

If this character is wrongly attributed to *A. africanus* and *H. habilis* hypodigms, three possibilities may explain why the mistake was made:

- A) The criterion of assigning characters to hypodigms was ambiguous;
- B) A non-ambiguous, good criterion, was wrongly used;
- C) Either KNM-ER 1805 or Stw 505, or both, do not belong to the presumptive *Homo habilis* and *Australopithecus africanus* species.

From my point of view, the criterion of assigning characters to hypodigms was right, and non-ambiguous. The presence of an illogical use of a good criterion cannot be disregarded in this case. However, I would like to point to the third possibility—the incorrect placing of a specimen in a particular species—as an almost universal risk to any phylogenetic analysis. This is the second kind of problems for a bottom-up approach that I referred to previously.

To decide whether some fossils either belong or not to a particular hypodigm is, sometimes, a controversial subject. For instance, to place the fragmentary cranial vault and face KNM-ER 2602 of Koobi Fora in the *A. afarensis* or *A. boisei* hypodigms is not an easy decision to make. The same might be said about Stw 53 and Sts 19 Sterkfontein specimens, which may be considered as either *A. africanus* or *H. habilis*. In all these cases, Strait *et al.*, (1997) place these argued-about fossils in one or the other species following prior studies, i.e., by means of a top-down scheme.

Choosing a set of species to construct their hypodigms is the third source of problems for a bottom-up procedure. If we use either a parsimony or a MLE criterion, data could, in principle, be characters or DNA

sequences, but in all cases data sets must be referred to species. When we talk about extant species, to assign an aligned DNA sequence or a set of characters to a species is a well-established assumption—we actually know what species are we talking about. However, when we are dealing with fossils, we are forced to attribute sets of characters to presumptive species. No definite criterion to identify a fossil species exists, which is not to say that species placed by different authors into the *Homo* genus are by no means the same ones.

Even the most meticulous study, like that of Strait *et al.*, (1997) starts with the need of choosing a set of taxa and the construction of hypodigms. Thus, bottom-up procedures start with some top-down assumptions: how many and what taxa will be taken into consideration, and what specimens belong to each of the taxa. Strait *et al.*, (1997) took extreme care to avoid this risk. They simply used an “alpha taxonomy” as a starting point, in order to be able to modify it after different analysis. This strategy has been followed several times in an attempt to avoid vicious circularity (see Cartmill, 1981), and it allowed Strait *et al.*, (1997) not only to initially accept the *Australopithecus robustus* and *Australopithecus boisei* taxa, but also to transfer them to the *Paranthropus* genus once the phylogenetical study was completed. Nevertheless, no phylogenetic study, as meticulous as it may be, will be free from the compulsory top-down operations of assigning specimens to species in order to define the hypodigm, and using functional hypotheses to compensate for trait bias.

Functional traits have often been used as an important tool in cladistics, either to get rid of the multiple considerations of functionally related characters (Strait *et al.*, 1997) or to decide the polarity of morphoclines (Gutmann, 1977; Skelton *et al.*, 1986). As Strait *et al.* say: “We are reluctant to conflate characters or construct complexes using untested functional inferences” (1997, p. 24). To use *tested* functional inferences is perhaps a better solution, but it clearly leads to top-down epistemological assumptions.

This is not a criticism of the paleontologists work, but a criticism to the naïve aim of constructing phylogenies in an extreme bottom-up way. In a paper headed “Recent advances in methods of phylogenetic inference,” Simpson wrote: “No one capable of effective phylogenetic studies starts with a *tabula rasa*. The early extreme pheneticists did in some cases postulate that as a principle, but none of them really followed it in practice and many have abandoned it in theory” (1975, p. 11). We are, thus, forced to accept circularity somehow. Some general top-down assumptions are needed as a starting point. Some of them will be identified as wrong by means of an accurate bottom-up study and they will, therefore, be discarded, giving way to new wide schemes. Those new schemes will be used in a top-down route to perform new detailed studies, and so on. Therefore,

general assumptions on the phylogeny of the human clade must be accepted as a compulsory principle to perform any taxonomic or systematic task. The cyclic nature of cladistic research recognized by Kluge (1997) seems to me to be a different way to express what I now hold.

Any source of evidence—like maximum likelihood methods applied to DNA and stratigraphy, as Marshall (1998) suggests—is welcome in order to guarantee the accuracy of cladograms and evolutionary trees. However, the intent of reaching this accuracy might be just wishful thinking. Siddall (1998) recently qualified the aim of describing correct ancestor-descendant relationships, reading ancestors in the fossil record, as a resurgence in the cult of the golden calf. Therefore, stratocladistics and stratolikelikelihood are severely criticized by this author. Anyhow, Siddall's (1998) arguments do not go further than Nelson's (1973), Cracraft's (1974) and Delson *et al.*, (1997) when they suggested that the inability to identify ancestors empirically is an axiom of the cladistic system. This being the case, Paleontology would end up by being unable to test any hypothesis about ancestors of extant species, or even check our whether any fossil taxon is actually different from an extant species or not.

Some epistemological misinterpretations are hidden, in my opinion, under these attempts to disqualify ancestor-descendant descriptions.

An extant species is a set of individuals that forms an isolated reproductive community. What then do we mean by a fossil "species"? When faced with a variety of fossil specimens, if we hold that they belong to a species different to any extant one, this may mean two things for us. Firstly (FS-A), that the members of this fossil species would be unable to breed—if it were possible—with their extant descendants. Cracraft's (1987) Phylogenetic Species seems to fit well into this first meaning. Cracraft defined the Phylogenetic Species as "an irreducible (basal) cluster of organisms, diagnosable distinct from other such clusters, and within there is a parental pattern of ancestry and descent." Nevertheless, fossil species also means, secondly (FS-B), that a variety of specimens form a species because they shared a distinct adaptive solution being expressed by a different morphology. Huxley's (1958) Grade, or Adaptive type, seems to fit well into this second meaning. As Collard and Wood (1999) say: "An adaptive type is a taxon with a more derived phenotypic pattern of organizational plan that is seen in the fossil record to replace an older taxon with less organizational plan." Very often, it is implicitly assumed that if we identify a FS-B, then it is also a FS-A, but this is not mandatory.

As Szalay (1999) holds: "Species are real, and they evolve [but] species taxa are formalized and at least temporally artificial chunks of lineages." Thus, fossil species are just mental constructs, an extrapolation of the biological concept of species to fossil specimens. If we place a particular extant individual in any species, we are holding a hypothesis that may,

somehow, be checked out. On the contrary, the first meaning (FS-A) of a fossil species cannot be falsified, since it is just an extrapolation drawn from the biological concept of species. Nevertheless, assumptions regarding fossil species in the second sense (FS-B) may be falsified by means of constructing cladograms and using a criterion, like that of parsimony, to check them out. To be able both to propose hypothesis in this way and also falsify them, we are then compulsory obliged—as a starting point, at least—to assume that some fossil species did exist. Top-down assumptions are thus unavoidable.

When we try to find the “correct” ancestor-descendant relationship, to focus fossil species using the FS-A meaning—a biological species placed in the past—is a hopeless task. We will not even be able to distinguish between direct and collateral ancestors. On the other hand, there is no epistemological barrier that impedes us from describing different fossil species—in the FS-B meaning—as adaptive solutions that preceeded our own. Actually, most of the human paleontology descriptions of bipedalism, scavenging/hunting/gathering, food-sharing, language, tools and so forth, and their morphological correlates, belong to this kind of concept of fossil species.

It is important to say once more that we cannot build character information intrinsic to a “species” belonging to the fossil record without some extrinsic aids, such as temporal distribution of the fossil, functional assumptions, and so on. This is a necessary consequence of the reductionistic’s logic work. Thus, we must choose between two ways. We could, on the one hand, get rid of any evolutionary assumption and describe raw fossil data as our only goal. On the other hand, we could accept the limits of the reductionistic task, describing “species,” constructing cladograms and proposing both phylogenies and scenarios, only as epistemological tools that will never provide a complete account of the history of lineages.

If we agree on this second way, what we desperately need is a general consensus on how the evolutionary process, at least in its more general levels at least, took place. If we cannot reach this kind of consensus to use it as a guide to human taxonomy, any proposed phylogeny will generate essential and unavoidable suspicion, any cladogram related to fossil species will lack credibility, and almost every new specimen found will give way to endless discussions. This, by the way, is a pretty good description of what we are currently faced with.

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