

# When is a cladist not a cladist?

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**Abstract** The term “cladist” has distinct meanings in distinct contexts. Communication between philosophers, historians, and biologists has been hindered by different understandings of the term in various contexts. In this paper I trace historical and conceptual connections between several broadly distinct senses of the term “cladist”. I propose seven specific definitions that capture distinct contemporary uses. This serves to disambiguate some cases where the meaning is unclear, and will help resolve apparent disagreements that in fact result from conflicting understandings of the term.

**Keywords** Cladist · Cladism · Phylogenetics · Systematics · Hennig Society · Parsimony

## Introduction

The term “cladist” has distinct meanings in distinct contexts. To some extent, individuals are aware of distinct meanings of this term and switch between uses as appropriate. However, there has been miscommunication and some confusion in the literature resulting from ambiguity in use. There appear to be correlations in usage with respect to discipline, literature, and possibly geography. In particular, communication between philosophers, historians, and biologists has been hindered by different understandings of the term in various contexts. In this paper I trace

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historical and conceptual connections between several broadly distinct senses of the term “cladist”. I propose seven specific definitions that capture distinct contemporary uses. This serves to disambiguate some cases where the meaning is unclear, and will help resolve apparent disagreements that in fact result from conflicting understandings of the term.

The need for clarification can be demonstrated by comparing classifications of systematists made by distinct authors. Most philosophical literature (e.g. Ereshefsky 2001; Sterelny and Griffiths 1999) follows Sober’s (1988, 2008) distinction between three (or four) distinct groups of systematists: pheneticists, evolutionary taxonomists, cladists, and (possibly) pattern cladists. Cladists base classification on genealogy only; pheneticists on similarity only; evolutionary taxonomists on both genealogy and similarity. Pedroso (2012) distinguished process cladists from pattern cladists and claimed that these are the two main schools of contemporary systematics.

In contrast, in this interdisciplinary journal *Biology & Philosophy*, Ebach et al. (2008) identified three groups of “cladists”: numerical cladists (type: Farris 1983), pattern cladists (type: Naef 1919), and transformed cladists (type: Patterson 1982). These are contrasted with one group of non-cladists:

(1) *Gradists* (type: Huxley 1940). Those who assume that ancestor–descendant relationships can be inferred from nodes on phylogenetic trees are most likely gradists. In addition to monophyletic groups, gradists would consider paraphyletic groups to be natural and discoverable, and at times designated as ancestors (Mayr 1942). Gradists are inspired by the works of George Gaylord Simpson and Ernst Mayr. We also include herein numerical taxonomists or pheneticists (Sokal and Sneath 1963), those who prefer similarity measurements and statistical procedures (e.g. Bayesian analysis, Maximum Likelihood, etc.), and those who belong to the “It doesn’t really matter” school of classification (Felsenstein 2003).” Ebach et al. (2008, p. 154)

Gradists that consider paraphyletic groups as natural and discoverable correspond to Ereshefsky, Sober, and Sterelny and Griffiths’ “evolutionary taxonomists”. However, none of these philosophers groups numerical taxonomists with evolutionary taxonomists. From the perspective of Sober’s classification, evolutionary taxonomists and numerical taxonomists are each distinct from cladists, and to group them solely on this basis would construct a “not-A” taxon (Eldredge and Cracraft 1980, p. 158). A paraphyletic grouping of this kind is problematic, to the extent that Ebach et al. intend to be providing a “cladistics” of systematists.<sup>1</sup> Ebach et al. also identified proponents of Bayesian analysis and Maximum Likelihood as Gradists, excluding them from any of the cladist categories. Many systematists who use similarity measurements, Bayesian Analysis, and/or Maximum Likelihood fit Ereshefsky, Sober, and Sterelny and Griffiths’ category “cladist”, and some might

<sup>1</sup> It may be that Ebach et al. intend only a cladistics of cladists, in which case a non-cladistic classification of other systematists might not be problematic. It is not clear, however, what use is served by identifying and naming the paraphyletic “not-A” group.

(depending on the meaning of “similarity measurements”) fit the category “pattern cladist”.

Lumping proponents of ML and Bayesian methods into the “non-cladist” category can have a denigrating effect given that evolutionary taxonomy and phenetics are frequently considered to be obsolete approaches, and philosophers accept the conceptual superiority of cladistics (e.g. Sterelny and Griffiths 1999, p. 200). On the other hand, as will be discussed below (“[One person’s poison](#)” section), in other contexts the label “cladist” can cast individuals and methods in a negative light. It is important to recognize that in some circumstances the label “cladist” encodes normative claims. In some contexts the label “cladist” is a mark of approval, and in others it carries negative connotations.

In what follows, I clarify the descriptive and normative dimensions of “cladist” by tracing the origins and development of distinct uses of the term “cladist”. This clarification will facilitate communication, particularly across disciplines, and will also shed light on the relationship between contemporary philosophy and a natural science.

I do not intend to classify individuals, ideas, or research programs. Rather, I clarify distinct things that speakers mean by the term “cladist”. If a classification were constructed on the basis of the distinct meanings, there would be substantial overlap between some of the groups. There would also be substantial disagreement about the naturalness of the classification, and substantial disagreement about which systematists belong in which group(s). There is probably greater diversity of views and arguments among those who label themselves “cladist” versus those who disavow that label. As Carpenter (1987) advised, it would be best to stop trying to classify systematists at all.

Rather than a classification or a field guide, I intend a foreign language dictionary. Which uses of “cladist” are foreign depends on the disciplinary, temporal, and philosophical location of the reader. As a philosopher, one foreign land to me is the discipline of systematics; as someone who did not experience debates of the 1950–1980s, another foreign land is this past. Although I summarize reasons for why the debates went as they did, and that the term “cladist” took on the meanings that it has, I intend to describe what speakers mean rather than prescribe any particular use as most appropriate. Some prefer to restrict the term “cladist” to one or a few particular meanings. I begin by delineating “cladist” in its historical context connected to Hennig’s phylogenetic systematics.

## **We are [almost] all cladists**

Cladist (i): A cladist is someone who accepts Hennig’s definition of “monophyletic”, or equivalently, that groups must be based on apomorphy rather than homoplasy, or plesiomorphy.

Cladist (i) now describes a historical group of systematists, and by extension people today who agree with the basic position of argued by those systematists. In his (1950) and (1965) works, and the (1966) rewrite and translation of the former, Willi

Hennig summarized the conceptual framework of modern phylogenetic systematics [building on the work of Naef (1919, 1921), Ziehan (1934), Zimmermann (1937), and others; see Schmitt (2013) and Rieppel (2016)]. The key principle is that the natural groups targeted by phylogenetic inquiry (above the species level) consist of an ancestral species together with all and only its descendants. Thus, the traditional group “fishes” is rejected on the grounds that some taxa considered fishes (lungfishes, coelacanths, and relatives) descend from a common ancestor shared with mammals, amphibians, and other non-fishes, but not shared with the other fishes (the Actinopterygii, Chondrichthyes, etc.). The monophyletic group (clade) Sarcopterygii includes lungfishes, coelacanths, and tetrapods; the clade Tetrapoda includes mammals, amphibians, and other terrestrial vertebrates.<sup>2</sup>

This innovation was resisted by many taxonomists, most prominently by adherents of two dissenting views: numerical taxonomy and evolutionary taxonomy. Numerical taxonomists did not dispute that monophyletic groups *sensu* Hennig are, in a theoretically important sense, natural. Many numerical taxonomists did not dispute that monophyletic groups *sensu* Hennig ought to be the targets of phylogenetic study. However, numerical taxonomists emphasized the difficulty in practice of identifying monophyletic groups as such. Traditional methods of distinguishing homology from non-homology are known to be fallible, and proposed methods of inferring ancestral character states are fallible. Observable characters are compared across organisms; patterns of similarity and difference are hypothesized to reflect patterns of descent. But characters yield conflicting signals. In the face of character conflict, the hypothesized pattern of descent requires that some observed similarities are not homologous. Given that there is no infallible way to identify true homology, numerical taxonomists increasingly came to interpret inferred patterns of similarity as just that. Claims that patterns of similarity reflect patterns of descent are made outside the context of systematics, properly speaking, according to this version of numerical taxonomy.

Evolutionary taxonomists explicitly rejected Hennig’s definition of “monophyly” (Hennig 1975; Mayr 1974). On this view, the natural groups that systematics targets may include groups that are paraphyletic *sensu* Hennig. A paraphyletic group consists of a common ancestor together with some, but not all, of its descendants.

The label “cladistic” was originally applied to Hennig’s system by opponents of these innovations (Mayr 1965; Dupuis 1984). Mayr criticized cladists for emphasizing cladogenesis, the branching origin of new groups, while ignoring anagenetic (phyletic) evolution, changes in lineages and among geographically distinct populations of species. In the 1960s–1980s, proponents of Hennig’s system accepted the label “cladist” because, in contrast to evolutionary taxonomists, they insisted that all taxonomic groups be clades: monophyletic groups, in Hennig’s sense of “monophyletic” (Nelson 1979, p. 13).

Cladists in this sense (i) won (Hull 1988; Donoghue 1990). Numerical taxonomists faded as an identifiable group, though the influence of numerical

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<sup>2</sup> Gauthier et al. (1989) defined Tetrapoda as a crown-group, such that extinct lineages that are more closely related to amphibians than to coelacanths are not tetrapods notwithstanding some of these lineages possess four feet rather than four fins. These extinct lineages are referred to as stem tetrapods.

taxonomy has been sufficiently important (Sterner and Lidgard 2014, 2017) that one of its champions has claimed (under an expansive definition of the term) that all modern systematists are numerical taxonomists (Sneath 1995). Natural groups above the species level may not be clades in groups subject to rampant lateral gene transfer, where phylogenetic trees often cannot capture both organismal and genetic patterns of descent (Doolittle and Brunet 2016). The naturalness of paraphyletic groups is still defended by some paleontologists (Carter et al. 2015), botanists (Brickell et al. 2008; Brummitt 2006, 2008; Hörandl 2006, 2007, 2010; Hörandl and Stuessy 2010; Zander 2008), and others (Holynski 2011; Vasilyeva and Stephenson 2008). Nonetheless, authors that recognize the naturalness of paraphyletic groups are presently an extreme minority in the systematics community.<sup>3</sup>

Later splits in the community of systematists were presaged by a difference in the source of cladistic methodology. Some systematists, including Farris, Kluge, and Eckart (1970) and Wiley (1975, 1981), explicated Hennig's methodology from Hennig's texts. Others, including Colin Patterson (1989, p. 472, 2011, p. 9) and Gareth Nelson (1969, p. 83; 2004, Bonde 2000, pp. 33–34; Patterson 1981, p. 8), learned cladistics through Lars Brundin (1966). Patterson viewed cladistics as a corrective to the deeply problematic practice of identifying individual fossils as direct ancestors of more recent groups (Nelson 2000). He was instrumental to the reception of cladistics via the 1972 symposium and edited volume *Interrelationships of Fishes* (Greenwood et al. 1973). Nelson read Brundin in connection with Leon Croizat's biogeography. Croizat's focus on vicariance served as a corrective to the problematic practice of inferring centers of origin based on the migration of supposedly younger versus older groups (Williams and Ebach 2008, pp. 119–122; Nelson and Platnick 1981, p. ix). Patterson and Nelson's interpretations influenced later systematists who adopted the label "pattern cladists" (see "[Anti-process cladists](#)" section, below).

Contemporary methods to identify and test hypotheses about relationships above the species level are collectively referred to as methods of phylogenetic inference. "Phylogenetic" is now understood exclusively in the sense of reconstructing groups that are monophyletic in the sense of Hennig (1966).<sup>4</sup> "Phylogenetics" is available as a term collectively for the component of the discipline of systematics that concerns inference about and representation of groups above the species level (Farris et al. 1970; Wiley and Lieberman 2011).

This (i) sense of "cladist" appears frequently in some contexts within the discipline of philosophy. However, this is not the only and may not be the most common way in which the term "cladist" is used by systematists today. When the context of inquiry clearly refers to the relevant historical period, systematists retain this sense of "cladist", but when the context of inquiry is the contemporary discipline of systematics, "cladist" can mean something quite different.

<sup>3</sup> Network approaches to describing and studying biodiversity may eventually subsume tree-based approaches (Doolittle and Brunet 2016). In that case, the terms "clade" and "paraphyletic" will no longer mean what they mean in the context of inferring trees of ancestry and descent.

<sup>4</sup> This was not always so. See for example Bather's (1927) remarks about phylogenetic classification.

## Old school cladists

Disputes between James Farris and Joseph Felsenstein were central to the subsequent evolution of systematics. As numerical taxonomy and evolutionary taxonomy faded from the scene, the use of parsimony versus maximum likelihood became a central debate in systematics. This dispute became notoriously personal for reasons that are not entirely clear (Edwards et al. 2016). Proponents of parsimony consider the tree that requires the fewest number of state changes in observed characters to be the best supported tree. Advocates of maximum likelihood consider best supported the tree that renders the observed data most probable, conditioned on a model which is itself tested via likelihood. In certain cases these two prescriptions yield conflicting trees. Felsenstein (1978) demonstrated that there are cases in which parsimony is statistically inconsistent—that is, as more data are added to the analysis, parsimony yields increasing support for an incorrect phylogeny. These cases occur when parameters (reflecting inequalities in branch lengths) fall within what is called the “Felsenstein Zone” (Huelsenbeck and Hillis 1993). Most commonly-used ML methods are less susceptible to this problem (cf. Tuffley and Steel (1997) for a ML method that will choose the same trees as parsimony, and is statistically inconsistent in the Felsenstein Zone). Farris (1983) claimed that such cases require assumptions about evolution that we can reliably expect will not occur in reality. In fact, such cases occur quite plausibly when nucleotide sequence data are used as characters. It is reasonable to expect that distinct lineages will each independently evolve from one state (e.g. guanine at a specified locus) to another (thymine at that locus) when there are only four possible character states. Reasonable models for analyzing the probability of character state changes first became available for nucleotide sequence data, and for this reason there is a loose connection to debates about prioritizing molecular versus morphological data. In fact, neither maximum likelihood nor parsimony is conceptually linked to the use of molecular versus morphological data.<sup>5</sup>

Some systematists argued for the superiority of parsimony on philosophical grounds (Farris 1986; Goloboff 2003; Kluge 1997; Siddall and Kluge 1997). David Hull recommended Popper to systematists at the American Museum of Natural History (Rieppel 2008), which was then (and is to some extent now) a bastion of parsimony. Walter Bock (1973) advocated grounding classificatory philosophy in the work of Popper. Whereas Bock argued that evolutionary taxonomy best conformed to Popper’s account of successful science, Wiley (1975), Platnick and Gaffney (1977), and others responded by using Popper’s work to defend phylogenetic systematics (cladistics (i)).<sup>6</sup> Hull had intended Popper to be a starting point for systematists’ engagement with philosophy (Oliver Rieppel, pers. comm.), but unfortunately, to some extent Popper’s work became enshrined to the point that adherence to (what is perceived as) Popperian principles is taken to be the end-all of solid philosophical grounding (Hull 1983; Rieppel 2008). Popper’s work (or

<sup>5</sup> Nonetheless, even today, in casual contexts I have observed proponents of maximum likelihood described as “molecular” people in contrast to proponents of morphological work.

<sup>6</sup> I thank Andy Brower for this point.

differing approximations thereof) became a frequent tool deployed by proponents of parsimony (Farris 2013; Kluge 2009; Vogt 2008; see de Queiroz and Poe 2001, 2003; de Queiroz 2014 for counter-arguments and Rieppel 2004, 2008 for analysis).

At some point, the term “cladist” attached to proponents of the use of parsimony in the context of these debates. This remains an extremely common use of the term “cladist” by systematists today; it is the dominant use in some contexts [e.g. it appears to be what is meant by the editors of the journal *Cladistics*—(Editors 2016)]. The phrase “old-school cladist” also serves to specify this use of the term by people who would use the term “cladist” in other senses (iii-viii below). “Parsimony cladist” refers to this type of cladist. The primary meaning is:

Cladist (ii): A cladist is a systematist who advocates the use of parsimony (in the sense of minimizing number of state changes) as generally or universally more reliable and/or more scientific than alternative methods of phylogenetic inference.

There is and has been a strong association between the Hennig Society (founded in 1980), the journal *Cladistics* (1985), and cladists in the sense of (ii). The methods that cladists (ii) initially rejected include phenetic clustering, additive tree methods, and character compatibility methods, but as Maximum Likelihood increased in prominence, cladists (ii) increasingly targeted ML. Over time, cladists sensu (ii) could be distinguished via sociological criteria (Hull 1988). Thus a third sense of “cladist” is

Cladist (iii): A cladist is a systematist who publishes in *Cladistics*, supports the Hennig Society, and otherwise socializes with individuals identified as cladists, either by self-identification or in the sense of (ii).

In recent years, *Cladistics* has published papers that do not fit the criteria for cladist (ii); and cladists (ii) certainly publish in other journals. Nonetheless, the association remains and the editors of *Cladistics* published an editorial advocating the use of parsimony; any other method would only be published if accompanied by a defense on “philosophical grounds” (Editors 2016).

Academic lineage plays a strong role here, but because of the existence of systematists who break ranks and switch from one side of the (evolving) debates to the other, academic lineage does not always reliably track cladists versus non-cladists sensu (ii) and (iii). It should also be noted that cladists (ii) and (iii) probably expend more energy arguing amongst themselves than against those who do not fit the cladist (ii) or (iii) descriptions (Andrew Brower, pers. comm.).

Over time, proponents of maximum likelihood improved their methods, molecular sequencing techniques advanced, and funding shifted to favor molecular methods (for reasons unrelated to the maximum likelihood versus parsimony debate). Many strict advocates of parsimony cladism adapted to this situation, in some cases using maximum likelihood in order to secure funding and to increase the chance of publication. Cladists innovated techniques unrelated to this dispute (e.g. simultaneous optimization of phylogenetic inference and sequence alignment; the parsimony ratchet for improving heuristic tree searches). So too did proponents of



other methods, as the science of phylogenetics evolved somewhat independently in distinct lineages. In fact terminology evolved independently, so that the same techniques and ideas came to have different names in the different camps (e.g., “explicit enumeration” = “exhaustive search”, “Bremer support” = “decay index”).

Eventually the distinction between cladists and non-cladists could no longer be captured by (ii), as members of the divergent groups of systematists increasingly focused on other issues. Some systematists would understand the sociological criterion (iii) as the dominant meaning of “cladist” today.

### Anti-process cladists

Some conceptual descent from parsimony versus max likelihood can still be recognized in some self-identified cladists who are not readily (or adequately) characterized as cladists in the strict (ii) sense of adhering primarily or exclusively to parsimony. There appears to be a conceptual connection via a deep concern about methods of inference grounded in statistical theory.

Cladist (iv): A cladist is a systematist who rejects the use of probabilistic inference in phylogenetics.

Skepticism of statistical inference procedures was deeply rooted in the parsimony versus likelihood debate, as revealed in arguments made by Siddall and Kluge, prominent proponents of cladism *sensu* (ii). Siddall and Kluge (1997) offer the following analogy, which accurately captures their central argument against the use of maximum likelihood as an exemplar of probabilistic methods.

Take, for example, the gambler’s fallacy: Roberto Alomar is batting 0.300. He comes to bat three times in a game and fails to get a hit. The naive gambler bets heavily on Alomar’s getting a hit on the fourth at-bat, because he is “due”. Our objective probabilist, like the likelihoodist, sees this differently and asserts that, because he is batting 0.300, he still has only a 30% chance of getting a hit, but this too fails to take into account the full scope of knowledge. In the first place, because Alomar failed to get a hit in his last three times at bat, he is actually batting 0.297; the probabilities have changed, because they are historically contingent phenomena [fn 1]. More to the point, Alomar either will or he will not get a hit and there is no probability that can be assigned to that one event: betting on one event alone is foolish.<sup>7</sup>

The problems with this argument are ably discussed in Haber (2005). What concerns us here is that the argument was made at all. If valid and sound, the argument would preclude predicting any individual occurrences at all, from weather

<sup>7</sup> In a footnote, Siddall and Kluge note that this example is flawed in that the drop in Alomar’s batting average depends on how many at-bats he has to start with. The drop in his batting average would be higher earlier in the season. The footnote contains two rounding errors and does not distinguish between at-bats and plate appearances (which might result in Palomar’s failure to get a hit without affecting his batting average), but these issues are irrelevant to the substance of the argument.



forecasts to spheres dropped from the tower of Pisa. Moreover, it would preclude any individual test of a hypothesis understood as a claim about individual occurrences as tokens of types. Fitzhugh (2016) explicitly endorsed this argument and conclusion, and denies that phylogenetic hypotheses are subject to empirical testing. Again, the argument and result can be extended to any scientific hypothesis at all. We have arrived at the polar opposite of a strict logical positivist view that testing of hypotheses is all that there is to science: the implication of Siddall, Kluge, and Fitzhugh's arguments is that there is no testing of hypotheses in science.

These arguments are traceable to philosophical arguments about the nature of historical scientific inference—that is, scientific claims about what the past was like. In an exchange with Michael Ruse (1971, 1973), Thomas Goudge (1961, 1967) argued that historical inferences do not make claims about phenomena understood as tokens of causal laws about types; instead, they make claims about causal relationships that are fundamentally singular.

What we seek to formulate is a temporal sequence of conditions which, taken as a whole, constitutes a unique sufficient condition of that event. This sequence will likewise never recur, though various elements of it may. When, therefore, we affirm 'E because s', under the above circumstances, we are not committed to the empirical generalization (or law) 'Whenever s, then E'. What we are committed to, of course, is the logical principle 'If s, then E', for its acceptance is required in order to argue 'E because s'. But the logical principle does not function as a premiss in an argument; the affirmation, 'E because s', is not deducible from it (Cf. Ryle 1950). Both s and E are concrete, individual phenomena between which an individual relation holds. (Goudge 1961, pp. 77–78)

Ruse (1971) pointed out that every event is “unique” and non-repeatable in at least the limited sense that each event bears unique spatiotemporal coordinates. The fact that an event is unique in this sense does not mean that a general law cannot be applied to the event. Ruse offered the example of a particular instance of a pendulum swing, which is the subject of general laws about the motion of pendulums. Ruse considered also the idea that “unique” indicates a particular combination of conditions, but again argued that this sense of unique does not bar the application of a general law, for the particular combination could recur somewhere.

The Ruse/Goudge exchange was fundamentally about causal ontology and what causal explanations must assume about causal ontology.<sup>8</sup> In contrast, the uptake of this type of argument in the systematics literature simply extended the claim that historical explanations do not apply causal laws to particulars. Phylogenetic inference is historical in that it makes claims about what happened in the evolutionary past. Philosophical literature on historical scientific inference typically focuses on claims about large-scale events that happened in the distant past, such as

<sup>8</sup> See Cartwright (1979, 1994) and Harré and Madden (1975) for accounts of causal ontology and causal explanation that support Goudge. Ruse's (1973) account builds on the covering law model (Hempel 1965).

the Snowball Earth hypothesis (Currie 2014; Turner 2007), the first colonization of land by vertebrates (Goudge 1961), and the end-Cretaceous mass extinction (Cleland 2002). Systematists deal with a broad range of cases, from deep divergences in the tree of life to relatively recent splits between lineages. Systematists are thus well-positioned to note the obvious point that the past didn't go anywhere: what happened one second ago is history (Asimov 1956). Fitzhugh (2006) extends the claim that historical inference does not apply general laws to particular historical events, to cover "history" in the sense of all inferences made up to the present nanosecond.

The distinction between historical science and experimental science is less clear than is sometimes made out (Cleland 2002; Whewell 1847, pp. 654–655). Nonetheless, there is a legitimate distinction between experimentally available phenomena versus long-ago historical phenomena that involve many diverse causal elements that are unlikely or impossible to re-assemble. This does not imply that processes cannot be modelled over historical timescales, or that these models cannot be tested against present and past phenomena.

**Cladist (v):** A cladist is a systematist who rejects the use of knowledge about process.

Cladists *sensu* (v) disagree with the conclusion of my above paragraph, with respect to applying evolutionary process knowledge to phylogenetic inference (see Scott-Ram 1990 for discussion). Arguments in support of this form of cladism frequently claim that the use of parsimony is justified by a fundamental epistemological principle, whereas process-based models require substantive and dubious assumptions about the world. The relevant epistemological principle is to avoid ad hoc hypotheses. All claims about putative apomorphies (character similarities thought to be derived) are taken, *prima facie*, as evidence of common ancestry (rather than convergent evolution), according to Hennig's auxiliary principle (Farris et al. 1970; Hennig 1966, p. 121). By minimizing the number of character state changes (i.e. maximizing cladistic parsimony), systematists posit the fewest ad hoc hypotheses of homoplasy necessary to match the character data to the inferred tree. A problem with this argument is brought out by considering its extreme form.

**Pattern cladist:** A *pattern* or *transformed* cladist is a systematist who claims that phylogenetic inference does not require and should not assume any theory of evolution.

The term "pattern cladist" was popularized by Beatty (1982); some proponents of the above claim (including Colin Patterson) preferred "transformed cladist". Pattern cladists disavow not just substantive knowledge about how evolution occurs, but that the fact that evolution occurs is necessary for phylogenetic inference (Brower 2000).<sup>9</sup> On this view, the claim that evolution occurs is a result rather than an assumption of inquiry in systematics. The problem with this view is that pattern

<sup>9</sup> The overwhelming majority (perhaps all) of pattern cladists were not and are not creationists. Some creationists have developed versions of "cladistic taxonomy" identifying "clades" supposed to be present on Noah's Ark (Ross 2014). I do not include these efforts in my taxonomy for the same reason that I cite them via website rather than journal: these are not scientific works.

cladists have no principled way to distinguish between monophyly, paraphyly, and polyphyly. The meaning of these terms includes irreducible reference to an ancestor (Rieppel and Kearney 2006; Rieppel 2010, p. 152 and footnote 1; see Platnick 1979; Williams and Ebach 2008; Schuch and Brower 2009, including glossary, for dissenting views).<sup>10</sup> Equivalently, the distinctions between apomorphy, plesiomorphy, and homoplasy cannot be made without reference to an ancestor.

This point undermines the arguments made in support of cladism *sensu* (v). Characters do not come pre-labelled in the world, and there is no theory-neutral way to identify and delineate characters (Rieppel and Kearney 2006). To take an example elaborated in Quinn (2016b), something as seemingly objective as the number of stamens on a plant specimen can variously be described as:

- Specimen q has six stamens
- Specimen q has an even number of stamens
- Specimen q has more than five stamens
- Specimen q has a ratio of 3 stamens: 2 petals

It turns out that the character ought to be scored so as to provide information about the ratio of stamens to petals. This is because the specimen belongs in a group whose other members exhibit the ratio 1 stamen: 1 petal. An ancestor of specimen q produced flowers in clusters of 3, with each flower bearing 4 stamens and 4 petals. In the species to which specimen q belongs, two of the flower clusters have been lost, but each left behind one stamen. The number of stamens is evidence that specimen q belongs with the 1:1 group, rather than with other groups that exhibit the ratio 2 stamens: 1 petal. That the number of stamens is six provided no evidence. There is no principled reason to treat the absolute number, six, (or any of the other descriptions listed) as meriting special epistemic status.<sup>11</sup>

<sup>10</sup> Rieppel (2010) explained the issue as the “pasta problem”: “take twenty-five different types of pasta, declare one (e.g. the thin spaghetti) as plesiomorphic, and do a cladistic analysis on them. The same can be done to taxa. What is the difference between applying cladistics to pasta or to taxa? As it cannot be the method, it must be the underlying ontology.” Consider a phylogeny wherein the true pattern of descent is [[A, B], C], D]. If I propose to group A and C to the exclusion of B and D, is my proposed group paraphyletic or polyphyletic? It is paraphyletic if I include an ancestor of B (for example, the branch between C and [A,B]). It is polyphyletic if I do not include an ancestor of B. The same argument can be framed in terms of sympleisomorphies versus synapomorphies. Williams and Ebach (2008, p. 18; Ebach and Williams 2004, p. 116) explicitly eliminate the poly- versus para-phyletic distinction. Patterson (2011) claimed that there is no need for this distinction, in which case the problem becomes to define what does and does not count as a “character” (homology claim) that co-constitutes the targeted pattern. Patterson’s (1981) arguments yield a coherent, conceptually sound method only in the event that Von Baer’s Law holds. Given that there are exceptions to Von Baer’s Law, the pattern of relationships that Patterson’s systematics targets may not match the pattern of branching evolution (i.e. phylogeny). The research program would have a principled way to distinguish characters; it simply would not line up with the goal of capturing phylogeny. In Patterson’s view, cladistics was not about phylogeny. See Williams and Ebach (2008) for a critique of Patterson’s tests of homology (pp. 63–81) and arguments that biogeographic analysis is necessary to distinguish homology versus non-homology.

<sup>11</sup> This example is taken from Candolle (1813), which raises an interesting historical question. Did Candolle implicitly work in an evolutionary context, notwithstanding that his arguments preceded the widespread acceptance of a theory of evolution? At minimum, Candolle’s arguments of this form, and his explicit statements that Adanson’s “objective” approach to characters was not objective (de Candolle, 1813, p. 71), indicate that he requires some theoretical foundation for taking characters as evidence of

There is substantial ambiguity about what counts as knowledge about process sensu cladist (v), and any reference to evolution for pattern cladists. At least for diagnostic purposes, it can be helpful to propose:

Cladist (vi): A cladist is a systematist who rejects the use of some large subset of maximum likelihood, Bayesian inference, permutation tail probability tests, constraint tree tests, simulations designed to assess reliability, and (perhaps) species tree methods.

Note that some cladists (vi) favor Bayesian inference, and some cladists (vi) use simulations designed to assess reliability. Cladists (vi) are diagnosed as sharing some substantive sub-set of all the listed criteria, rather than by any one or few necessary and sufficient properties. Is there a conceptual unity to this list? It might be that many of these items make substantive use of probability theory as part of phylogenetic inference and/or hypothesis (dis)confirmation. In at least some cases the more direct link is to Kluge's "principle of total evidence", which has been used to reject any subdivision of data in the course of phylogenetic inference (even in the case that all the data are considered through repeatedly sampling subsets of the total data). Initially deployed to support one particular form of parsimony analysis against another (Kluge 1989), the principle of total evidence was subsequently used to support parsimony methods versus maximum likelihood (Kluge 2001a, b, 2004; see Rieppel 2005 for discussion; Cf. Wheeler 2006).

More recently, the principle of total evidence has been cited as a reason to be critical of statistical binning (which is necessary for species tree methods to be computationally tractable), because this procedure partitions the available evidence (Gatesy et al. 2016; Simmons and Gatesy 2015). Cladists sensu (vi) may reject species tree methods on this ground regardless of whether statistical binning involves a substantive use of probabilistic inference in the sense of cladists (iv).

## One person's poison

A blatantly partisan characterization of "cladist" can be identified:

Cladist (vii): A cladist is a systematist who critiques other systematists' work on methodological grounds, while ignoring deeper conceptual problems with his or her own preferred procedures.

Underlying this characterization is the thought that cladists (vii) are resistant to change and seek to invalidate newer methods that better reflect phylogenetic theory by pointing to limitations and errors in application. From the opposite side of the

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Footnote 11 continued

natural relationship. What that theoretical foundation may have been is not relevant to my points about contemporary systematics, whose conceptual framework presupposes the concept of evolution (de Queiroz 1988; Hennig 1966, p. 22; Hillis 2004; Sober 2008, pp. 334, 352; Wiley 1981, pp. 1–2). See Quinn (2016a, c) and Winsor (2015) for discussion of inference in pre-evolutionary systematics and how systematics became historicized.

partisan fence, this supposedly reactionary attitude is in fact scientifically responsible.

Setting aside the charge of reactionary attitude, (vii) remains partisan in that the debates are fundamentally about what counts as a deep conceptual problem versus a mere methodological problem. What is ultimately at issue is a disagreement about what concepts, methods, and assumptions are fundamental components of phylogenetic theory versus “merely pragmatic” assumptions that are unavoidable simplifications made by individual methods. Use of the term cladist (vii) to characterize proponents of any method requires that one prefer a certain distinction between methodological assumptions and theoretical principles.

Cladists (vii) are perceived as trying to cover over conceptual flaws by making arguments that problematic cases rarely occur. The parsimony-likelihood debate has sometimes been presented as hinging on whether homoplasy is rare. More precisely, a critical issue in Farris and Felsenstein’s exchanges was whether cases in the Felsenstein Zone occur frequently, rarely, or never at all. Critics of cladists (ii) view Farris as ignoring the problem that there is no theoretical justification for preferring the assumptions made by parsimony over those made by likelihood, given that parsimony can be viewed as an over-parameterized likelihood model (Goldman 1990; de Queiroz and Poe 2003; de Queiroz 2004). The empirical assumption that cases in the Felsenstein Zone are rare hides the conceptual problem by denying that it would ever practically affect analyses.

That is not to say that parsimony requires no assumptions at all; it presumes, one might say, that Felsenstein’s models are unrealistic. But as that assumption seems generally agreed upon, that is not much of a criticism of parsimony. (Farris 1983, p. 16)

Felsenstein’s original (1978) models were subsequently modified to better match knowledge and theory about molecular evolution. Following these modifications, systematists for the most part abandoned Farris’ assumption.

## Cladists and philosophers

A final characteristic to note is that cladists have frequently appealed and continue to appeal to the philosophy of science to support their arguments. Hennig was very much concerned to ground the conceptual framework of systematics in an appropriate philosophy of science (Rieppel 2016; Schmitt 2013). In defending cladism (ii), Farris (1983) drew on Popper and on Sober (1975). The cladist (iii) journal *Cladistics* published a widely-read editorial in February 2016 that stated:

The epistemological paradigm of this journal is parsimony. There are strong philosophical arguments in support of parsimony versus other methods of phylogenetic inference (e.g. Farris 1983).

...

If alternative methods give different results and the author prefers an unparsimonious topology, he or she is welcome to present that result, but should be prepared to defend it on philosophical grounds.

In keeping with numerous theoretical and empirical discussions of methodology published in this journal, we do not consider the hypothetical problem of statistical inconsistency [i.e. Felsenstein's arguments] to constitute a philosophical argument for the rejection of parsimony. All phylogenetic methods, including parsimony, may produce inconsistent or otherwise inaccurate results for a given data set. The absence of certain truth represents a philosophical limit of empirical science. (Editors 2016).

Siddall and Kluge's (1997) cladist (iv) arguments regarding linking probability theory to phylogenetic inference cited no less distinguished a list than Berkeley, Carnap, Einstein,<sup>12</sup> Hacking, Hempel and Oppenheim, Hume, Kant, Lakatos, Mill, Nagel, Popper, Quine, Reichenbach, Russell, Sober, and Watkins. Fitzhugh (2006) argued against many of the methods rejected by cladists *sensu* (vi) on philosophical grounds, by developing an account of phylogenetic inference as inference to the best explanation.

Engagement between biology and philosophy is certainly desirable in general, but we must be careful of the character of the engagement. The danger to avoid is reaching for isolated chunks of philosophy, ignoring both contrary philosophical views and appropriate context, with the express aim of defeating identified theories and methods. Such an approach can too easily become a misplaced appeal to authority.

It is my hope that this paper will facilitate further constructive engagement between philosophers and systematists. In any case, the distinctions that I have drawn should help to navigate the array of circumstances in which persons and methods are referred to as "cladists".

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<sup>12</sup> Einstein was a philosopher as well as a physicist. See Howard (2005), Norton forthcoming.

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