

Character Analysis in Cladistics: Abstraction, Reification, and the Search for Objectivity

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Abstract The dangers of character reification for cladistic inference are explored. The identification and analysis of characters always involves theory-laden abstraction—there is no theory-free “view from nowhere.” Given theory-ladenness, and given a real world with actual objects and processes, how can we separate robustly real biological characters from uncritically reified characters? One way to avoid reification is through the employment of objectivity criteria that give us good methods for identifying robust primary homology statements. I identify six such criteria and explore each with examples. Ultimately, it is important to minimize character reification, because poor character analysis leads to dismal cladograms, even when proper phylogenetic analysis is employed. Given the deep and systemic problems associated with character reification, it is ironic that philosophers have focused almost entirely on phylogenetic analysis and neglected character analysis.

Keywords Characters · Cladistics · Phylogenetics · Morphology · Abstraction · Reification · Biological theory · Epistemology · Causation

How are we to recognize the “true” characters of organisms rather than imposing upon them arbitrary divisions that obscure the very processes that we seek to understand? ...No issue is of greater importance in the study of biology.

—Lewontin 2001, p. xvii

Are characters natural units or artifacts of observation and description? In both systematics and ecology, there is often a considerable gulf between observables and the units that play causal roles in our models.

—Fristrup 1992, p. 51

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“Garbage in, garbage out”

–Pimentel and Riggins 1987, p. 201; Mishler 2005, p. 59

1 The Argument

Identifying, individuating, and measuring the basic ontological units of biological systems is irreducibly important to the life sciences. Over the last three decades, significant philosophical energy has been invested in two types of ontological questions regarding basic biological units: *what is a species?* (e.g., Wilson 1999) and *what is a unit or level of selection?* (e.g., Lloyd 1988; Okasha 2007) More recently, in the wake of the growth industry of evolutionary developmental biology, another sort of question has caught the attention of the philosophically curious: *what is a homology?* (e.g., Brigandt and Griffiths 2007) This paper is an attempt to analyze a question related to the third one: *what is a character?* My philosophical analysis will emphasize the importance of developing objectivity criteria for the invariably theory-laden abstraction of characters. If such criteria are not employed, it becomes all too easy to inappropriately reify characters. The life science that I shall focus on is morphology-based cladistics.

This paper is structured as follows. Section 2 presents the philosophical background and methodology. In particular, a philosophical methodology that investigates the actual practice of science rather than, for instance, abstract conceptual analysis will be defended (of course the two sorts of methodologies are not mutually exclusive).

Section 3 provides an introduction to cladistic analysis. Following a number of other authors, I distinguish between (1) *character analysis* and (2) *phylogenetic analysis* as two temporally and logically distinct stages of cladistic analysis (e.g., Jardine 1967, 1969; Stevens 1984; Rieppel 1988, 2004; de Pinna 1991; Hawkins et al. 1997; Thiele 1993; Williams and Siebert 2000; Rieppel and Kearney 2002; Mishler 2005; Richter 2005; see also Neff 1986, Fig. 1, p. 115; Bryant 1989, Fig. 1, p. 216; Brower and Schawaroch 1996).¹ I use this distinction for the general thesis of this paper: *a careful and correct character analysis is indispensable for the subsequent inference of good cladograms*. That is, even the best inferential, syntactic methods for phylogenetic analysis cannot rescue bad data gleaned from careless or unreflective character analysis—“garbage in, garbage out” (Pimentel and Riggins 1987, p. 201; Mishler 2005, p. 59). Put differently, phylogenetic analysis can always construct a cladogram, from *any* data. It is because of this that we must worry about the quality of the data.

Section 4 outlines the specific themes of abstraction, reification, and the search for objectivity in character analysis that emerged from Sect. 3. Section 4 thus presents my understanding of what is at stake in cladistic analysis. Section 5 makes explicit six objectivity criteria that are employed by workers in morphology-based cladistics. In Sect. 6, I conclude by briefly exploring the philosophical themes of

¹ In this paper I will bracket issues regarding classification and taxonomy. My concern is with the character analysis and the phylogenetic analysis of cladistic inference.

subjectivity and objectivity in scientific knowledge. I do this by discussing how my project differs from Richard Richards' "subjectivist" philosophical investigation of cladistic analysis (Richards 2002, 2003). My "objectivist" account emphasizes *causal grounding* (criterion 5) and *inter-disciplinary communication* (criterion 6) as two particularly important objectivity criteria in character analysis.

Let us explore the central argument in more specific detail. *Abstraction* is central to the identification, individuation, and measurement of every character, from petal color to the relative position of a skull bone. This abstraction is *always* theory-laden since it is guided by (1) theoretical ontological commitments about what could possibly count as a character, and by (2) theoretically-determined operational methods (i.e., instruments, heuristics, and tacit knowledge) for individuating, distinguishing, measuring, drawing, and counting characters. Because of the fundamental role played by theory-laden abstraction in character analysis, we must be vigilant about taking each and every one of our abstracted characters too literally. As a matter of fact, some abstractions, some characters, are not true reflections of the world. (Here "the world" is the *empirically inaccessible yet true* Natural System or, if you prefer, the Tree of Life.) Instead, some of the abstracted characters are merely reifications. They are misleading homoplasies, or objects and properties of organisms that have no biological meaning. They are the outcome of our abstraction process taken pathologically too far. That is, these characters are thought—(1) stubbornly or (2) naïvely and without critical awareness—to exist, despite the fact that they have not been evaluated according to any objectivity criteria. The dangers of character reification loom large (see the first two epigraphs).

So, given (1) the necessary ubiquity of theory-laden abstraction *and* (2) the existence of real biological systems with parts and processes, and their properties, how can we in practice actually distinguish *irresponsibly reified characters* from *objectively real characters*? This is where the rigorous and empirically-based objectivity criteria for character analysis enter (e.g., topology, special similarity, and series of intermediate forms). These criteria for "primary homology" assessment (sensu de Pinna 1991), which we will explore in detail, provide normative guidance as well as heuristics for a healthy abstraction process. They permit us to justify only some characters as real (for phylogenetic purposes). Thus, we have the means of separating true from reified characters and hence of attaining some objectivity in our ongoing systematic classifications of the world of biological species and higher taxa.

2 Philosophical Background and Methodology

The philosophical methodology of this paper is to analyze the epistemic and methodological theorizing practices employed by phylogenetic systematists when they explicitly try to distinguish real from artifactual/reified characters. The following questions are addressed in this context: (1) In which ways are characters actually abstracted? (2) Is it possible to abstract characters in a theory-free manner? (3) Which sorts of criteria do systematists use to objectively verify (or falsify?) the characters—the primary homologies—that they have putatively identified, individuated, and measured?

I explore actual practices rather than engage in highly abstract analyses, conceptual or otherwise, because one way to productively answer the ontological question “what is a character?” is by focusing, *in vivo*, on the scientific practices that *themselves* attempt to answer this question. For our philosophical purposes, the practices can be empirically gleaned directly from the literature and from prominent workers in cladistics. Practice-based philosophical investigations of character analysis could nicely complement, perhaps even subsume, more theory-based general analyses of the character concept (e.g., Wagner 2001). At any rate, the two sorts of analyses are not mutually exclusive.²

Interestingly, practice-based analyses invite us to not draw a sharp line between ontological and epistemological/methodological questions. In fact, I shall assume that giving a philosophical account of how ontological questions in science are actually answered will require investigating both (1) the power and limitations of epistemic and methodological practices and (2) the structure of the world. I argue that (1) and (2) are inseparable and that a good place to begin studying (2) is by the ways in which (1) in fact allows us (imperfectly, perhaps) to determine (2) and, furthermore, at least under some interpretations, to *co-construct* (2).³ The suggestion, then, is that philosophers can usefully address ontological questions by *tracking how epistemically-located ontological commitments are employed—at times in a reified, and at other times in a justified manner—in actual science*.

Moreover, while I certainly accept the questions of the first two epigraphs and believe in a complex and dynamic biological reality, I emphasize that the distinction between “natural units” and “artifacts” must not be drawn naïvely: natural units can only be discovered and characterized through our abstraction processes, rife with limitations. *Character abstraction is irreducibly crucial to character analysis*. Thus, one contribution the philosopher can actually make to the community of systematists is to suggest ways for these scientists to self-reflexively and critically

² Moreover, both can be descriptive as well as normative. Indeed, the project of this paper is ultimately normative. The objectivity criteria developed in Sect. (6) are gleaned from good practice and are norms for how a cladist *should* engage in proper character analysis. (I thank Elliot Sober for pushing me on this.)

³ Although I am one of its defenders, the latter interpretation of the co-construction of epistemology/methodology and ontology is, strictly speaking, optional for the argument of this paper. For instance, a strong philosophical realist who distinguishes epistemological from ontological matters (e.g., Devitt 1991) can still read this paper for insight into how scientists go about *discovering* characters that exist in the world independently of science. Under this realist light, practice-based investigations of scientific reasoning are useful particularly because they indicate the myriad ways in which *biased* scientists produce representations that deviate from a true or ideal description of the world. Some strong realists (“the world is difficult to know” realist) could then find my project interesting because it gives us a handle on the many difficulties we always encounter in the discovery process. *Other* strong realists, however, would of course be free to downplay my project because it does not address ontological questions directly (whatever exactly that would mean), either in science or in a philosophical rendition of science, but instead “conflates” ontological and epistemological matters by focusing on practices. A final note in this context. Strong realism is not the only sort of theory-based philosophical analysis available. Other sorts of theory-based investigations insist on a much more nuanced relation—social, Kantian or otherwise—between epistemology/methodology and ontology (e.g., Kuhn 1970; Goodman 1978; Putnam 1981; Friedman 1999). Thus, the (i) theory-based versus practice-based philosophical analysis distinction is emphatically not co-extensive, let alone identical with, the (ii) epistemology/methodology versus ontology dichotomy on which the strong realist intently insists. That is, a theory-based investigation need not be premised on distinction (ii).

develop methods to *overcome* biases in character abstraction while simultaneously admitting that their own character abstraction practices are necessary and powerful. A focus on epistemically-located ontological commitments, then, allows us both to address ontological question “what is a character?” (previous two paragraphs) *and* to provide ways to fine-tune actual scientific abstraction practices. In fact, this paper is part of a larger project on the promises of abstraction, and the limits of pathological abstraction—of *abstractionism*—in the biological sciences (e.g., Winther 2006a, b, 2008).

In short, I will use a practice-based philosophical approach focusing on epistemic/methodological matters in order to show how objectively real characters are distinguished from inadequately reified ones in morphology-based systematics.

3 Cladistic Inference: Character Analysis and Phylogenetic Analysis

In this section, I explore some key features of cladistic practice. I distinguish between two stages of cladistic analysis: (stage 1) *character analysis* and (stage 2) *phylogenetic analysis*. In so doing, I point to the central problem of cladistic inference: *an inappropriately and carelessly implemented character analysis leads, even with a subsequent high quality phylogenetic analysis, to problematic cladograms*. Unfortunately, this problem has not received sufficient attention in the philosophical literature on cladistic analysis. After introducing basic aspects of cladistic inference, two solutions to this problem are considered: (i) increasing the sheer number of characters used and (ii) employing objectivity criteria to identify appropriate primary homologies and only using those characters for stage 2. I shall primarily defend (ii).

3.1 The Basics

Characters are the fundamental data of cladistics. The first stage of cladistic analysis is the phase of *character analysis* (de Pinna 1991; Rieppel 1988, 2004). In character analysis, we would ideally like to abstract and choose, from the very beginning and before we start inferring any cladograms, a suite of characters that are homologous and therefore phylogenetically informative. These are the “true characters of organisms” (Lewontin). As it turns out, we rarely attain this best-case scenario. However, provided we employ objectivity criteria of primary homology assessment (to be explored in Sect. 5), we are very likely to find phylogenetically rich characters that will be corroborated as secondary homologies in stage 2.

In the second stage of cladistic analysis, *phylogenetic analysis*, character and character state data arranged in a data matrix⁴ are used to infer the most

⁴ Strictly speaking, there is an important link between character analysis and phylogenetic analysis: *character coding*. That is, even once we have abstracted characters and character-states, we need to write them out in proper form for a data matrix. There is significant debate regarding the best way to formalize characters: e.g., whether we should use “present” / “absent” or focus primarily on positive statements of character-state properties [e.g., Pleijel 1995; Fitzhugh 2006, 2008 (see options A-F on p. 275 of 2006); Sereno 2007; see also Freudenstein 2005 who usefully distinguishes characters from character-states in

parsimonious cladogram based on that data (Sober 1988, 2008; Wiley et al. 1991; Rieppel 1988; McManus Guerrero 2006, McManus Guerrero, this issue). The most parsimonious cladogram(s) is the one (are the ones) that employ(/s) the smallest number of character state transitions in its branching arrangement of nested taxa. One way to understand the determination of the branching order of the cladogram is through the principle of generality: character *a* is more general than character *b* if the extensional set of species indicated by (the derived state⁵ of) character *b* is a proper subset of the extensional set of species indicated by (the derived state of) character *a* (Eldredge and Cracraft 1980, pp. 36–37; De Queiroz 1985; Rieppel 2004, p. 12; see also Nelson 1978, p. 339 ff.). Character *a* thus provides the basis for a larger group (branch) of which *b* is a proper sub-group (a nested sub-branch). For example, in vertebrates, the character of “four-chambered heart” picks out a larger and proper super-set of the group determined by the character “hair”. Moreover, this smaller group is co-extensive to the group picked out by “mammary glands”. Now, if the (derived state of) character *a* is shared by all species but one in the data matrix, this suggests that that one-out species is a sister taxon to the group consisting of all the other species with *a*. Moreover, if the (derived state of) character *b* is shared by, for instance, half of the other species, these species would then be grouped together. With more characters, we thus get an inclusive hierarchy of groups within groups (Darwin 1859, p. 411; Hennig 1966).

The key problem with *phylogenetic* analysis is that *even good characters are not mutually consistent*. That is, focusing on different characters, together with their character-states will give us different groupings. To follow our example, a

Footnote 4 continued

terms of their exhibiting either “paralogous” or “orthologous” relationships (sensu Fitch 1970), respectively, with other characters or character-states; the titles of Pimentel and Riggins 1987 and Hawkins 2000 suggests that they will write about primary homology assessment, but in fact they each end up addressing character coding]. Character coding as a problem is clearly important, but well beyond the scope of this paper as it concerns the *link* between character and phylogenetic analysis, rather than character analysis *sensu stricto*. Put differently, I am concerned with the abstraction and reification process that occurs prior to writing out the characters and character-states in the data matrix. Of course, I realize that the two problems (i.e., “primary homology”/character assessment problem, and coding problem) are not independent (e.g., Stevens 2000), but conceptual progress can still be made by focusing exclusively on the former. And certainly the former cannot be reduced to the latter (contra Fitzhugh and Sereno)! Another issue I will not address here is the *polarization* of characters (e.g., Patterson 1982; Nixon and Carpenter 1993; Brusca and Brusca 2003). Since methods of polarization (e.g., outgroup comparison) do not affect the *nature* or *quality* of the characters, but attend to which of two or more character-states is postulated to be ancestral/synapomorphic (a topic crucial to phylogenetic, but not character, analysis), this important topic is not germane to this article.

⁵ The establishment of the polarity of a character state—i.e., the determination of a particular state as either ancestral or derived—is done through ontogeny or outgroup comparison, or both. Under ontogenetic analysis, the character state that appears first during development is considered the primitive character state (e.g., a two-chambered as opposed to a four-chambered vertebrate heart). Under outgroup comparison, the character state that is most frequent in groups other than the ones being investigated is considered the primitive state (see Radinsky 1987, p. 6).

different (derived state of) character c could indicate a different species as the one-out from all the other species. Or a different (derived state of) character d could re-divide in half the group of species identified from character a in a manner completely distinct from character b . How do we solve the problem associated with mutually inconsistent characters? This is where parsimony analysis enters. Given a set of characters that are not mutually consistent (i.e., do not produce a single neat hierarchy of ever more inclusive groups), we choose the grouping that 1. *incorporates the largest number of characters possible that provide a consistently inclusive hierarchy of groups within groups* (called “compatibility” by Farris and Kluge 1979; Felsenstein 1982) or, perhaps more realistically, 2. *incorporates all characters, trading them off against one another such that, potentially, “no individual character may be entirely compatible” with the cladogram* (see Felsenstein 1982, p. 381). Many advocates of parsimony analysis see the principle of generality as an outcome, rather than a method, of phylogenetic analysis. I will not adjudicate between these phylogenetic optimization criteria here as that is beyond the scope of the paper (for a critical evaluation of these and other options for optimization, see Sober 1988, Chap. 5 “Parsimony, Likelihood, and Consistency”, Sober 2005, 2008, Chap. 4 “Common Ancestry”, and Williams and Ebach 2007, Chap. 11 “Character Conflict”). In fact, further details of the inference methods for deriving the inclusive hierarchy cladogram in the appropriate manner—including character weighting, tree rooting, maximum likelihood versus parsimony and so forth—have been usefully explained elsewhere and will not be further rehearsed here (see, e.g., Sober 1983, 1988; Hull 1988; Rieppel 1988; Wiley et al. 1991; Schuh 1999; Felsenstein 2003; McManus Guerrero 2006; McManus Guerrero, this issue).

Now, the cladogram that expresses the best inclusive hierarchy according to the chosen optimization criterion, tells us which of our chosen characters—our primary homologies—*actually are* homologies. This is because each primary homology is also a “miniature phylogenetic hypothesis all by itself... and can be tested against other postulated homologies.” (Mishler 2005, p. 60) That is, those primary homologies that pass the congruence test (Patterson 1982, 1988; Rieppel 1988; Brooks 1996) are “secondary homologies” (sensu de Pinna 1991)—i.e., synapomorphies (nodes) of the inferred cladogram. The congruence test occurs through “reciprocal illumination” in which each postulated, primary homology is tested against all other postulated homologies, i.e., against the cladogram (see Rieppel 1988, pp. 57, 60; Brooks 1996, p. 4).

There are thus two tests of homology: stage 1 “observational” testing producing primary homologies, which is my concern in this paper, and stage 2 “inferential” testing where we assess whether primary homologies are actually synapomorphies of an inferred cladogram, and thus secondary homologies. As we shall see further below, the main point here is that if we perform a poor stage 1, we are doomed to infer an inadequate cladogram. Thus, finding, agreeing upon, and implementing good criteria for character analysis is paramount. In light of this, it is a shame that almost all philosophical effort on cladistic inference has been invested in the second stage.

3.2 Three Distinctions Pertinent to Cladistic Inference

Before we turn to the central problem of cladistic analysis in Sect. 3.3, I need to address some conceptual problems that lurk in this discussion of the two stages of cladistic inference. These problems surround three distinctions:

- (1) systematic pattern versus evolutionary process
- (2) inclusive versus divisional hierarchy
- (3) priority of character analysis versus priority of tree analysis.

I briefly attend to each in order to show that the danger of character reification looms large *regardless* of the meta-theoretical position one takes with respect to systematics, classification, and evolution.

The first distinction was pressed particularly by the “pattern cladists” (Platnick 1977; Nelson and Platnick 1981; Patterson 1981; Brady 1985; Williams and Ebach 2007; for a more “neutral” defense of the pattern versus process distinction, see Bonde 1977, 1996; Rieppel 1988; see Beatty 1982; for a contemporaneous viewpoint which coined the very term “pattern cladism”, see Hull 1988 for a review). The pattern cladists asked: is it sufficient, for purposes of cladistic systematic knowledge, to find the appropriate representation of the inclusive hierarchy, or must we also somehow *explain* the hierarchy? We could, they argue, postulate descent with modification—genealogy—as the explanation for the Natural System hierarchy. However, since this would add an explicit biological evolutionary ontology, we are not obligated, for the purposes of systematic knowledge, to take this further, mechanistic step. After all, hierarchical pattern is logically separable from hierarchical process.

There are two reactions to this view. First, the distinction is downplayed, and sometimes even denied, by the prevalent views of “evolutionary” or “phylogenetic” cladism (see Beatty 1982; Hull 1988; Ereshefsky 2001), which holds that pattern cannot be understood without the theoretical and ontological context of process-based evolutionary theory (i.e., speciation through descent with modification). Second, others have suggested that while a distinction exists, the two are complementary and that it is in fact impossible to investigate one without the other (e.g., Hennig 1950, p. 26, 1966, p. 15 and (#3) on p. 23; Rieppel 1988, Chap. 6 “Being and becoming: the conflict of pattern and process”, Rieppel 2006b, p. 383). It is important to point out that the problems associated with character abstraction and reification examined in this paper remain equally acute under any of the three perspectives on the pattern/process distinction. After all, there cannot be a pre-given, automatic, and absolutely objective source of characters, even for just the pattern of the Natural System. In short, character analysis *should be* of deep concern to each of the three perspectives.

The second distinction remains an ongoing “confusion in cladism” (Williams 1992; Rieppel submitted). Patricia Williams succinctly distinguished between the Linnean and the divisional hierarchy. Although her choice of terms is infelicitous (the former should really be called the “inclusive hierarchy” for purposes of generality, Rieppel, personal communication), her descriptions are apt:

In the *Linnean hierarchy*, biological relationships are expressed as relationships of inclusion. As one ascends from the lower, restricted levels of the

hierarchy to the upper, more general levels, each lower level is included in the one above it. (Williams 1992, p. 135, added; see Fig. 1a, b)

These examples indicate that the *divisional 'hierarchy'*, is formed by the process of the division of one entity into two over some span of time, and by that process alone. (p. 139, emphasis added)

Whatever explanation one uses, however, the *divisional 'hierarchy'* nowhere expresses inclusion relationships. Species A does not include species B and C; it produces B and C by division. Parent clones do not include their offspring; they produce them by division. Sexual parents do not include their children; they beget them. The relationships are all unidirectional and non-inclusive. They cannot be correctly represented by nested boxes. (p. 140, emphasis added; see Fig. 1c, d)

This is a central distinction (for commentary see Williams et al. 1996). Hull (personal communication) refers to it as a dichotomy between “subsume, subsume, subsume” and “split, split, split”. This distinction has yet to be resolved. Many contenders (of both “pattern” and “phylogenetic” cladist camps) simply fail to see a distinction and, instead, confuse:

- (1) a graph-theoretical representation of nested, subsumed sets of taxa (i.e., a cladogram representing conceptual and inclusive “part-whole” relations (Fig. 1b), which is itself logically equivalent to a set of nested Venn diagrams (Fig. 1a))

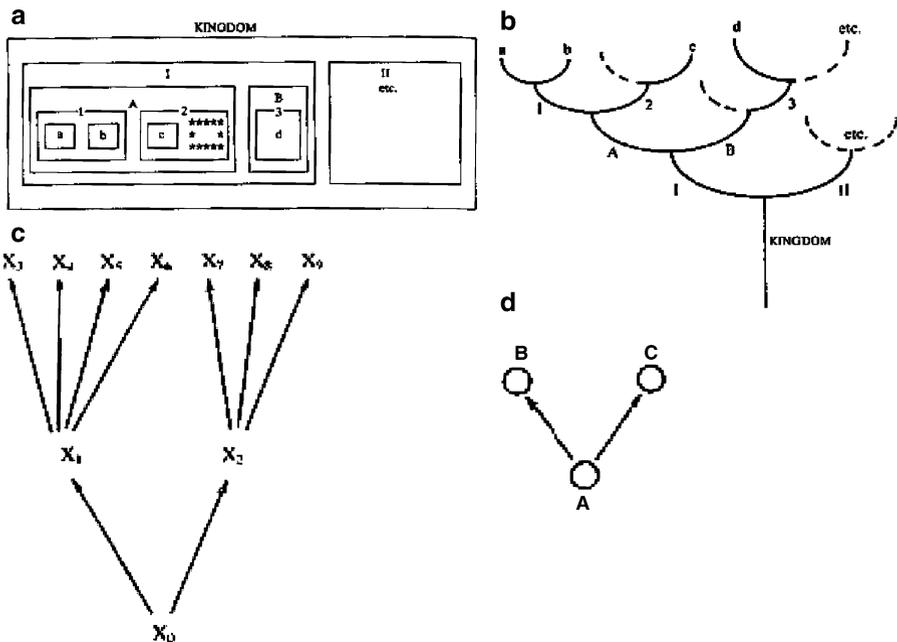


Fig. 1 From Williams (1992). See text. Reprinted by kind permission of Springer Science and Business Media

with

- (2) an exclusive processual mapping of genealogical splitting (as a model for this splitting, consider the parent-offspring relation (Fig. 1c, d)).

In my above explanation of the principle of generality, I focused on the inclusive hierarchy, while fully endorsing the importance of the divisional hierarchy. The point here is that, again, regardless of one's commitments to the existence and relation between these two hierarchies, character analysis remains a problem because of the perennial risk of character hypostasis. First, potentially problematic characters, and character-states, are the data that allow us to erect ever-inclusive groups (inclusive hierarchy). Second, even if we are strong process-oriented realists about the divisional hierarchy, the only way that we can infer—i.e., know something—about that hierarchy is through the methodology of character abstraction giving us, first, an inclusive hierarchy that we subsequently use as a *model* for the divisional hierarchy. In short, there is no escaping character analysis. There is no “view from nowhere” from which we can glean the true Natural System or Tree of Life (even granting that such a System or Tree exists⁶).

Thus far, I have remained agnostic and open regarding the first two distinctions. Each extant perspective on each distinction is important and coherent. Moreover, and this is the crucial point for the purposes of this paper, character reification is a danger regardless of the position taken on distinctions (1) or (2). However, regarding the last distinction—between priority of character analysis and priority of tree analysis—I will be committal. Regardless of the approach we take to the first two distinctions, we are *never* obligated to give the tree priority (contra Härlin 1999). Thus, Härlin's (1999, p. 499) view that “characters themselves do not have anything to do with the choice of phylogenetic hypotheses” goes against good cladistic practice. Characters have *everything* to do with the choice of cladograms, however these are interpreted (i.e., (1) pattern-wise or processually, (2) inclusively, and/or divisionally). Characters are the empirical basis, the admittedly theory-laden data, upon which we base our cladograms.

⁶ A word about “true System or Tree” or “true cladogram”. As argued in Sect. 2, I adopt a sort of epistemically-conditioned realism here, rather than an instrumentalism. However, the argument in this section goes through regardless of one's commitments in the realism debates. There is presumably a fact of the matter about the pattern and process of the evolution of life; there is presumably a true System or Tree. This is so regardless of how difficult it is to infer it or whether there is an “irreducible” human-abstraction component to it. I trust that the reader will grant this. (See Vergara-Silva, this issue, for discussion and healthy skepticism about such a view.) Now, given that there is a fact of the matter about pattern and process, do we need to use explicit methodologies and criteria for character analysis in order to get close to this cladogram? This paper argues that we should and can have recourse to objectivity criteria for character analysis (or else we will miss the mark). In contrast, many others (solution 1, see below) argue that even granting the in principle existence of a true cladogram, explicit criteria are not necessary in our search for it. A final point. I am here concerned specifically with those regions of the universal history of life where *cladistic assumptions* hold (e.g., vertical inheritance and branching modification with descent, as is the case for chordate evolution). It is at best unclear what the true System or Tree would be for domains of the history of life (e.g., early microbial evolution) where cladistic assumptions do not hold in particular because there is *horizontal gene transfer* (e.g., Woese 2000; Doolittle and Baptiste 2007; O'Malley and Dupré 2007). I bracket this important issue here.

3.3 The Central Problem of Cladistic Analysis and Two Solutions

What then is the exact nature of the problem with character analysis? Will reliable methods of phylogenetic analysis not give us correct cladograms, independently of the characters used? What is all the fuss about? The problem is that the nature of the data used for cladogram inference does matter. *Phylogenetic methods cannot fix bad data*. After all, cladograms are constructed using data matrices containing both morphological and molecular characters.⁷ If we happen to choose enough characters that are misleading—i.e., that are homoplasious or biologically meaningless—we will infer cladograms that deviate, to greater or lesser extents, from the true cladogram. That is, if we hypothesize the wrong primary homologies, the inferred secondary homologies will themselves be erroneous. To put it metaphorically, phylogenetic analysis does not have enough “judgment power” to support all of the inference necessary for a correct representation of the Natural System. To be absolutely precise, *no* phylogenetic method, whether it be (1) cladistic (i.e., maximum parsimony, explored in this paper), (2) maximum likelihood, (3) Bayesian inference, etc., can rescue poor characters. Bad input data will produce incorrect and biased phylogenies, regardless of phylogenetic method employed. Mishler reminds us of the dictum “garbage in, garbage out” (see also Pimentel and Riggins 1987, p. 201), and further notes “no model of the evolutionary process can be brought to bear successfully if the data matrix does not represent cogently argued character and character-state statements.” (Mishler 2005, p. 59) To focus, again, on cladistic phylogenetic analysis: reciprocal illumination (testing for congruence) will not work appropriately given bad data.

How exactly do poor characters distort the phylogenetic analysis? Consider the case of grouping cetaceans with salmoniformes rather than with ursidae simply because cetaceans “look” more like salmon than like bears—and with respect to many characters potentially postulated in an unreflective character analysis they do! Now contemplate the following groupings: [cow (trout, lungfish)] versus [trout (lungfish, cow)]. For these two cases, which are the correct classifications? Are those the “intuitive” ones? Indeed, these two counter-intuitive examples motivate the fact that using homoplasious or meaningless characters in phylogenetic analysis can lead to dismally wrong cladograms.

More generally, whenever we choose suites of poor characters, we still infer cladograms because one can *always* infer a cladogram (stage 2) from any conglomerate of characters. Such cladograms, however, deviate significantly far from the real ones (e.g., Brooks 1996, pp. 3–6; Sanderson and Donoghue 1996, p. 69, note 6 above). Thus, even with correct syntactic manipulation of data, if the input data are corrupt, we will not infer an adequate output representation.

In the cladistic literature there are at least two families of suggestions for how to solve the central problem of cladistic inference (i.e., that an inappropriately

⁷ Although I focus on morphological data in this paper, I cannot here avoid talking about molecular data. As we shall see, the latter are hardly a magical bullet for cladistic analysis (Patterson 1988; Patterson et al. 1993; but see Scotland et al. 2003).

executed stage 1 would lead, even with adequate stage 2 methodology, to hopelessly incorrect cladograms):

- (1) increase the sheer number of characters used in stage 2, or
- (2) employ objective criteria to identify appropriate primary homologies and only use those characters for stage 2.

The first solution holds that a character analysis is unnecessary as long as we have sufficient numbers of characters. Thus, it accepts that impoverished characters are problematic since they can lead to inaccurate cladograms, but rather than focus on the *nature* of the characters, it entails that we should focus on the *number* of the characters. Effectively, it endorses a view of “the more the merrier.” In contrast, the second solution argues for constant vigilance regarding primary homology assessment—the nature of the characters must be evaluated using objectivity criteria so that we can separate out primary homologies from reified characters. We will analyze each solution in turn.

The first solution, which is related to the “requirement of total evidence” (Kluge 1989; Lecointre and Deleporte 2005; see de Queiroz et al. 1995 for a review) has received by far the most attention. The basic idea is that particularly molecular studies will provide us with myriad new characters. As long as we have sufficient amounts of data, homoplasious or biologically meaningless characters will bias the cladograms in radically different directions and hence the sum total of errors introduced by reified characters will “come out in the wash”. Thus, due to what could be called a “law of large numbers of independent error deviations,” we need not engage in character analysis of primary homologies using objectivity criteria (e.g., Hillis et al. 1994; Hillis 1996; Bremer et al. 1999; Hillis and Wiens 2000; Poe and Wiens 2000; Felsenstein 2003; Scotland et al. 2003). In effect, many workers in molecular systematics believe that they do not need to know much, if anything, about the biological processes in which the gene sequences they use as character data are involved.

The second solution has received less attention and tends to be defended by biologists employing primarily morphological characters (e.g., Patterson 1988; Patterson et al. 1993; Smith and Turner 2005; Rieppel 2008 accepted; Rieppel and Kearney 2002, 2007; N. Bonde, O. Rieppel, D.M. Williams, F. Vergara-Silva, personal communication). These biologists emphasize that there are also reification problems with molecular data. For instance, there are “multiple sources of homology problems unique to molecular data, including gene duplication, horizontal transfer, and exon shuffling.” (Smith and Turner 2005, p. 167, citing; Hillis and Wiens 2000, p. 12; see also Mindell 1991; Mishler 2005⁸). Moreover, these cladists oppose the morphology-critical view that morphological data have “maxed out” their relative value for systematic classification because they are pertinent primarily to large-scale taxonomic resolution and are therefore not likely to increase the corroboration or accuracy of finer-scaled cladograms (for a

⁸ Mishler (2005, p. 665) provides a useful “pro and con” table for molecular and morphological data. Molecular data have at least two disadvantages: they have neither “complexity and comparability” nor “many possible character states.”

morphology-critical view, see, e.g., Scotland et al. 2003). In fact, advocates of testing for primary homology support employing objectivity criteria *both* on morphological and molecular data. We should not just abstract any possible character from our specimens; we need to use normative criteria.

Advocates of the second solution hold that character analysis is at least as problematic and important as phylogenetic analysis. I have perhaps gone further by calling the character analysis problem *the* central problem of cladistic inference, and provocatively relegated the admittedly important phylogenetic analysis problem of optimization criteria (for resolving character consistency) to a secondary status.

These two solutions are not necessarily in opposition. Although their emphasis certainly differs, the ideal is to combine the two: *the quality of the product of phylogenetic analysis is improved proportionately to the increase in numbers of good characters*. Unfortunately, the prevalent bias in the literature is towards the first solution. Both because we cannot be sure that character reifications will come out in the wash (how would we ever know that if we fail to consider it a real and present danger worthy of our attention?), and because the second solution to the central problem of cladistic analysis deserves more of a hearing, it is the one articulated and defended in this paper.

To summarize, two strong quotes will help put the argument of this section in relief:

1. A brief review of the structure of cladistic analysis will quickly reveal why an explicit, progressive method of character analysis is so important to the quality of our phylogenetic hypotheses. ...The cladistic analysis itself is relatively trivial: it is only summarizing the information already entirely contained within the characters. ...The important questions in a phylogenetic study lie in the basic, fundamental, empirical study of morphology, physiology, behavior, or any other source of comparative information about the organisms: what are, in fact, the character distributions? (Neff 1986, p. 116)
2. One could easily argue that the first phase of phylogenetic analysis is the most important; the tree is basically just a re-presentation of the data matrix with no value added. This is especially true from a parsimony viewpoint, the point of which is to maintain an isomorphism between a data matrix and a cladogram. We should be very suspicious of any attempt to add something beyond the data in translating a matrix into a tree! (Mishler 2005, p. 57)

Although these quotes exaggerate—e.g., different phylogenetic methods do not always give the same cladograms and there are often various best cladograms possible, so phylogenetic analysis is not trivial, nor does the cladogram “only summarize the information already entirely contained within the characters”—there are important elements of truth in them. They certainly make the point I have wanted to stress: character analysis is a difficult and important task and doing it incorrectly can lead to inaccurate cladograms. Moreover, increasing the sheer *quantity* of characters cannot be the entire solution to character analysis (stage 1). We must also evaluate the *nature*, *quality*, and *content* of the data (Table 1).

Table 1 Table summarizing the two central problems of cladistic analysis

Type of analysis	Central problem	Problem description	Problem solution
Character analysis (Stage 1 of cladistic analysis)	Bad characters	Abstracting bad, <i>retified</i> characters leads to skewed cladograms (“garbage in, garbage out”)	<ol style="list-style-type: none"> 1. “The more the merrier”—use many characters 2. Employ objectivity criteria 3. Use both (1) and (2)
Phylogenetic analysis (Stage 2 of cladistic analysis)	Inconsistency of good characters	Sum total of good characters of a data set do not support the same cladogram	<p>Use some total of good characters to build cladograms according to various methods (with respective optimization criteria):</p> <ol style="list-style-type: none"> 1. Maximum parsimony 2. Maximum likelihood 3. Bayesian analysis

In my view, the “bad characters” problem is *the* main problem of cladistic inference

4 Abstraction, Reification, and the Search for Objectivity: An Account of Character Analysis

I have been arguing that character analysis (i.e., character identification, individuation, and measurement) is always an act of theory-laden abstraction. There are multiple ways in which theory operates in character abstraction:

- (1) each systematist emerges out of *theory-laden (a) traditions* and *(b) fields*. She thus learns to abstract particular sorts of characters for specific organisms. (a) Traditions involve teachers and schools, e.g., in studies of Cirripedia, Darwin 1854 still sets the tone (e.g., Newman and Ross 1976; van Syoc and Winther 1999). (b) Fields include comparative anatomy, functional morphology, developmental biology, and molecular genetics; a comparative anatomist will abstract out different sorts of characters than a molecular geneticist (Winther 2006c),
- (2) the social context of (1), together with creative individual insight, provides the background for two interacting aspects of abstraction: (a) (theory-laden) *operational methods* (i.e., instruments, heuristics, and tacit knowledge) for individuating, distinguishing, measuring, drawing, counting, etc., characters; (b) (theory-laden) *ontological assumptions* about what could even possibly be a character,
- (3) a preferred cladogram may *already be known* and hence characters may be selectively chosen that corroborate that cladogram (for an example referring to two competing theories/cladograms of snake phylogeny, see Rieppel and Kearney 2001).

I am particularly concerned with (2). That the abstraction process ineliminably and invariably involves theory-laden operational methods and ontological assumptions is not problematic per se. At any rate, it would be impossible to eliminate theory from the abstraction process. Methodological error, however, arises when explicit objectivity criteria for guiding and justifying this abstraction process are not used. These criteria are effectively *norms* for character analysis. They allow us

to distinguish those characters that are reasonably and robustly real from those that are irresponsibly reified. Thus, attention to these criteria of primary homology assessment is essential for good cladistic practice. These criteria can be readily gleaned from the literature and will be explored in the next section (e.g., Wiley 1981; Patterson 1982, 1988; Rieppel 1988; de Pinna 1991; Wagner 1994; Richards 2002, 2003; Kearney and Rieppel 2006; Rieppel and Kearney 2001, 2002, 2007; Sereno 2007).

Under my analysis, the objectivity of the criteria involves three aspects:⁹

- (1) the criteria are publically shared, and further tested and refined, in the community of systematists (e.g., Longino 1995, 2002; Kusch 2002),
- (2) the criteria guide abstraction processes that actually interact with real objects and properties under study,
- (3) the criteria permit distinguishing between real and reified characters.

That is, employing objectivity criteria provides us with guidance and heuristics for the abstraction process and, ultimately, provides the justification for why some abstracted characters are *good* or *proper* characters (rather than hypostatized characters), useful for subsequent phylogenetic analysis.

5 Cladistic Practice: Towards Objectivity Criteria in Character Analysis

Let us turn to abstraction, reification, and the use of objectivity criteria in character analysis in the actual work of morphology-based cladists.

5.1 Abstraction and Reification

The identification, individuation, and measurement of any character is an act of theory-laden abstraction of the properties of real biological systems. In their co-authored papers, Rieppel and Kearney explicitly address this issue. Regarding the grasping of similarity, they note that

recognition of ‘the same but different’ ... in a primary conjecture of homology will necessarily be based on an observation that entails a conceptual element sometimes referred to as ‘abstraction’ or as a ‘subjective element in character delimitation.’ (Rieppel and Kearney 2002, p. 64)

In order to recognize similarity, and thus the sharing of characters, a variety of processes of abstraction must occur (see also Rieppel and Kearney 2001, p. 113; Stevens 2000). For instance, certain sorts of character variation must be ignored (1) abstract *away from*. Moreover, the *essential properties* of parts or organisms, which are the characters on which we focus [e.g., the relative position of a part or its special similarity (Remane 1952)], must also be recognized (2) abstract the *core properties*. These properties are precisely the characters that we postulate as primary homologies and that are the *same* across taxa. Indeed, Patterson calls the “1:1 correspondence”,

⁹ These correspond to two of the four aspects of objectivity in Lloyd 1995 (see also Lloyd 1996).

or the sameness of character, established through a “similarity test” (one of his three criteria of homology) an “(3) *abstracted* identity” (Patterson 1988, p. 605, emphasis mine). Finding similarity thus amounts to identifying the same abstracted character (of parts or organisms) across different taxa. Moreover, abstraction can also be used to (4) *distort* specimens productively to find the appropriate identical parts (Rieppel and Kearney 2002, p. 70, give the example of Pierre Belon who hung up a bird skeleton in the correct pose for emphasizing that certain bird and human bones are homologous; consider also tomography imaging of fossil skulls, which can distort particular cross-sections to highlight relative position and adult transformations). There are thus at least four modes of character abstraction: 1. away from, 2. identify core properties, 3. abstracted identity, and 4. distortion.

Although these types of character abstraction can, at times at least, be “subjective” as Rieppel and Kearney note, this is probably not the best way of describing this complex inferential process. In fact, if the various modes of abstraction follow the criteria to be detailed below, then the process is made objective and stops being perniciously subjective. And while further philosophical work is required to fully map out the abstraction process, promising frameworks can be found in Cartwright (1989) and Jones (2005). Following Cartwright and Jones, it seems plausible to argue that at least in comparative biological science, abstraction involves both (1) the *omission and subtraction* of myriad properties from the objects of study and (2) the identification of *core and idealized* properties that capture the essence (i.e., the typologized essence, see Love, this issue) of those objects. This abstraction is qualitative and structural.

Can this abstraction ever be theory-free? As we saw above in Sect. 4, character abstraction is embedded in social and individual contexts that are replete with operational methods and ontological assumptions. These methods and assumptions are theoretical to the core. Theory learned, as well as theory developed through individual insight, will make a difference to which characters are identified; in addition, the character definition adopted might also make a difference (see Richards 2002, 2003). Moreover, even putatively “theory-free” methods are rife with theory, as Kearney and Rieppel point out regarding the pheneticists:

Even to apply a punch-card (Sneath and Sokal 1973, Fig. 3–1) to the automatic scanning of characters in a purely operational/algorithmic approach still presupposes theory, namely the theory that morphological homologs can be discovered by ignoring anatomical complexity. (Kearney and Rieppel 2006, p. 376)

As a further example of implicit and ubiquitous theory-ladenness, Kearney and Rieppel give this one: “Coding suites of developmentally correlated characters as independent entries in a data matrix... takes a theoretical stand, which is to *a priori* reject the hypothesis of developmental correlation.” (2006, p. 375) There is a common theme to these two examples: regardless of how morphological and developmental characters are abstracted, we are always committed to a theory. There is no standing outside of theory (Richards 2002, 2003). Thus, the dangers of reification loom large when we are blithely oblivious to the constraints of the biases and limitations of a theory (and every theory has them).

5.2 Objectivity Criteria

How then can we separate reified from real characters? In what follows, I start with an apology regarding the very definition of “character.” I then turn to the six criteria of primary homology assessment: (1) relative position (topological), (2) special similarity, (3) series of intermediate forms, (4) conjunction, (5) causal grounding, (6) inter-disciplinary communication.¹⁰ Four of these are rather well accepted. I shall defend the last two criteria as very important additions to an already strong list. Our search, as cladists seeking objectivity in our character ascriptions, could be radically strengthened by taking these two criteria seriously.

Here is the apology. As mentioned in Sect. 2, my investigation focuses on practices rather than on conceptual analysis. Thus, I will not be able to review the myriad definitions of characters provided by a variety of workers (for character definitions, see, e.g., Wiley 1981, pp. 115–117; Ghiselin 1984; Colless 1985; Frisrup 1992, 2001; Thiele 1993, pp. 279–283; Sereno 2007, p. 566, who identifies 15 definitions). In fact, the differences among these definitions may be less severe than they at first appear; many character definitions seem to be complementary. Moreover, Colless’ (1985, p. 230; see Frisrup 1992) trichotomy differentiating (1) character-attribute (e.g., “has brown wings”), (2) character-part (e.g., “wings”), and (3) character-variable (e.g., “wing color”) is the one that I endorse.

What is the relationship between the concepts of “character” and “homology”, two key concepts of this paper? Obviously this is not an easy question, but my suggestion is that *the referents of adequate primary homology claims simply are parts, their characters, and their character-states*. (These correspond, respectively, to Colless’ “character-parts”, “character-variables,” and “character-attributes.”) After all, appropriate characters and character-states are the entries in the character matrix. We assume the 0 s (or 1 s, etc.) of specific columns of the matrix to be equivalent—i.e., the same—*because* we have used the objectivity criteria (discussed below) for identifying them. In addition, we assume that the 0 s (or 1 s, etc.) are, ideally, synapomorphies (recall Hennig’s auxiliary principle). Of course this latter assumption is defeasible, but in practice we do presume primary homology claims (of character-variables) to be synapomorphies unless proven otherwise.

I have argued that homologies should be fleshed out as parts and (especially for the purposes of the data matrix) their characters and character-states. Is the reverse true? Must all biologically meaningful characters be actually, or even potentially, homologous? To put the question bluntly: can other sorts of true characters be found that are not based on the objectivity criteria here explored *and* the phylogenetic (synapomorphy) criteria of sameness/similarity? If so, are such characters really true characters? Such questions are among the most difficult for those of us concerned with biological reality and its hierarchical natural order. There is a broad gamut of answers. Some cladists seem to answer these questions in the negative, preferring to

¹⁰ I have not employed the interesting character rejection criteria from Poe and Wiens (2000) (see also Sereno 2007), such as high character variation or substantial missing data, because their criteria do not get at primary homology claims or character analysis as such. Rather, they are investigating something more like character coding (see note 4 above). Stevens (1991, 2000) discusses some of the reification problems entailed by such criteria.

equate “natural” characters only with evolutionarily relevant ones (e.g., Eldredge and Cracraft 1980, pp. 43–44). Hennig was broader and claimed that there were various types of characters that could be used to construct different types of ordered systems: “groups of individuals may pertain to a physiological (homoiothermy, for example), ecological (parasites), phylogenetic (insects), or any other constructed system.” (Hennig 1966, p. 8) However, he argued that despite this diversity, a phylogenetic (cladistic) system should, and had to, serve as “the general reference system of biology” (1966, p. 239, see also 9–27 ff.) Others go much further, and hold that different sorts of natural kinds and natural kind hierarchies “cross-cut” one another, with no need for an ultimate subsumption; hence it would be perfectly reasonable to defend the naturalness of ecological, phylogenetic, physiological, and genetic characters, and natural kinds (e.g., Khalidi 1998; Dupré 2002; Hacking 2007; Rieppel 2008).

It would be beyond the scope of the paper to further address the naturalness of any characters or natural kinds that are defined by criteria that do not appeal to synapomorphies. But it is, again, important to observe that whatever our intuitions about the naturalness of such characters may be, the problem of character reification in cladistics remains. On the one hand, if we think true characters have to be synapomorphies, or at least that we should have had *good reasons* to believe that they could have been synapomorphies (i.e., they should meet our objectivity criteria), then the argument of this paper is not in the least affected. On the other hand, even if we think that there are *other* sorts of criteria for defining and assessing characters, those characters would have their own forms of abstraction,¹¹ but the subset of characters pertinent to the cladistic system would *still* suffer from the central problem of cladistic inference here explored. For the purposes of this paper, then, “primary homology” or “secondary homology” *and* “character” are used co-extensively.¹²

We will now turn to the six criteria for primary homology (i.e., character) evaluation. One of the first explicit articulations of character analysis in a cladistic context was Wiley (1981). In his book, Wiley invests approximately 60 pages (pp. 115–176) on criteria and examples of character analysis. He uses the term “recognition criteria of homology” to describe what we call “criteria of primary homology”. The criteria he employs are taken from Remane (1952): (1) the criterion of *relative position*, (2) the criterion of *special quality of structures*, and (3) the criterion of *continuance of similarity through intermediate forms*. Each one has to do with similarity and their application is an empirical matter (e.g., Rieppel 2006b; Rieppel and Kearney 2002). Let us explore each in turn, as presented in Wiley’s book.

¹¹ And, I suspect, reification, but showing that would be part of another project.

¹² I realize that some will disagree because they will only want to make “secondary homology” and “character” co-extensive, under the cladistic paradigm. I will simply say that the motivation for employing objectivity criteria is that they give us good characters—i.e., ones that are highly likely to be synapomorphic. Recall [Sect. 3] that I take issue with those who abstract any character whatsoever, without applying the objectivity criteria. Put differently, using objectivity criteria brings primary homology claims closer to secondary homology affirmations.

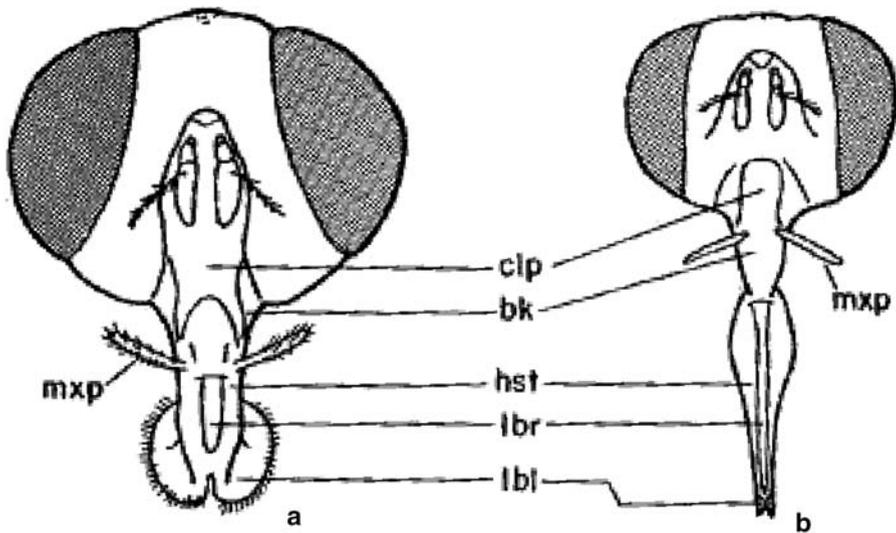


Figure 5.6 Remane's criterion of topographic position, II. Frontal views of (a) a sponging fly (*Musca*) and (b) a piercing fly (*Stomoxys*). The labeled mouth parts have the same relative topographic positions although they differ in shape and, in some cases, function. Abbreviations: bk, rostrum; clp, clypeus; hst, haustellum; lbr, labrum; lbl, labellum; mxp, maxillary palp. (Modified from Borror et al., 1976.)

Fig. 2 From Wiley (1981), p. 132. This figure is useful for illustrating the first criterion of relative position. See text. Reprinted by kind permission of the publisher from Wiley E.O. 1981, *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*, p. 132, New York: John Wiley & Sons. Copyright © 1981 by John Wiley & Sons, Inc

The first one (1) is perhaps the single most important criterion for character analysis. The relative positions of parts are used to map the *same* part across taxa. Once such homologous parts have been identified, their characters and character-states can be evaluated. Consider Fig. 2. The homologous mouth parts of a “sponging” and a “piercing” fly can be identified through their relative positions. We subsequently abstract pertinent characters for each of these types of parts.

The second criterion (2) of special quality is sometimes used to rescue ascriptions of primary homology that could have been lost because the first criterion was not met. Alternatively, it can falsify statements of primary homology when the first criterion is met. Thus, it can certainly enter into conflict with the first criterion. Of course, there are also many cases where the two criteria reinforce each other, but, as Wiley points out, these are not the “interesting” cases (1981, p. 134). As an example of conflict between the two criteria, Wiley observes that:

The vertebrae of bowfins and teleosts have the same positional relationships to other parts of the body such as the neural and haemel arches and the body myomeres... Yet each has different embryological development and their special qualities are different as a result of this different embryological development... (Wiley 1981, p. 134)

The details of the body parts are not important here. But note that despite meeting the first criterion, the parts are not considered homologous *sensu stricto*.¹³ Thus, with the first two criteria as well as with the others, the cladist has some theoretical flexibility in primary homology assessment. However, the criteria do give her normative guidelines.

The third criterion (3) establishes the homology of parts together with their characters through the use of intermediate forms. That is, two parts may initially seem dissimilar and thus not homologous, but once intermediate forms of these parts are found in the ontogeny or fossils of other obviously related taxa, the systematist can postulate a “series of intermediate forms” of the *same* part together with its *changing* character-states and, even, (some) characters (Remane 1952; Wiley 1981). These intermediate stages “can be inferred from the ontogeny of the organism stages originally compared, or they may be supplied by paleontology” (Hennig 1966, p. 94; see also Nelson 1978). As is the case with all primary homology claims, such an empirically assessed series is defeasible and needs to be corroborated through phylogenetic analysis as an actual genealogically meaningful “transformation series”, i.e., as a secondary homology claim (Stevens 1984; Grant and Kluge 2004; Rieppel 2006a). Certain intrinsic problems must also be addressed (e.g., Stevens 1984, p. 398, notes that “the two ends [of the series] ...may have nothing in common at all”). But this criterion can be exceedingly useful in helping us find fairly objective intermediate form series that are corroborated as transformation series.

Let us be more specific. A classic example of a series of intermediate forms that is also a phylogenetically meaningful transformation series is the evolution of the mammalian ear (Wiley 1981, p. 137; Fig. 3). The three bones of the mammalian middle ear (Figs. 3, 4)—the stapes (s), incus (i), and malleus (m)—are homologous respectively, to the branchial (hm), quadrate (q) and articular (a) of amphibians and therapsids. The story is complex (e.g., Radinsky 1987; Rieppel personal communication). The first two gill arches—the “visceral arches”—of agnathans (“jawless” fish) were transformed over evolutionary time to become part of the throat skeleton and stapes of non-mammalian tetrapods, and, eventually, the three bones of the middle ear of mammals. This evolutionary transformation from gill arch to middle ear has a developmental grounding. In fact, the parts are quite similar early in development. Each one of these three bones, then, is effectively the *same* bone across the specified vertebrate taxa. Thus, in order to abstract characters for each one of these three bones for our character matrix, we identify and measure different character *states*, across taxa, of the same part (i.e., bone). Indeed, the only way we could postulate and corroborate that we have the same bone in different taxa is by identifying the correct intermediate forms.

¹³ They could be considered homologous at a higher level of resolution: qua vertebrae of vertebrates, in general. Rieppel and Kearney 2006 make this exact point (p. 101). It is generally true that homology claims need to be relativized to a particular level of comparison: e.g., bird and bat wings are not homologous qua wings, but they are homologous qua tetrapod limbs. For the purposes of this paper, and for stipulating the same “character”, I will focus primarily on low, concrete levels of resolution (e.g., wings rather than tetrapod limbs) and will not further discuss this important issue.

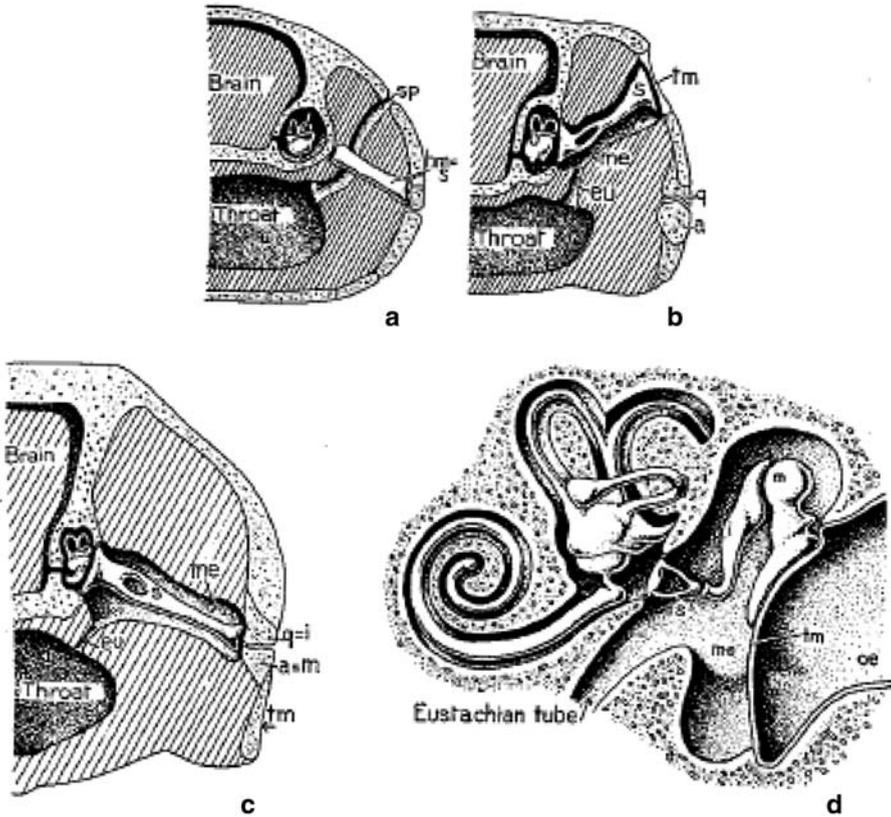


Figure 5.10 Remane’s criterion of intermediate forms, the evolution of the mammalian ear: Cross sections through hypothetical skulls of (a) a fish, (b) an amphibian, (c) a reptile, and (d) a mammal. Abbreviations: a, articular; cu, eustachian tube (homologue of part of the spiracle); hm, hyomandibular (homologue of stapes); i, incus (homologue of quadrate); m, malleus (homologue of articular), me, middle ear cavity (homologue of part of the spiracle); q, quadrate; sp, spiracle; tm, tympanic membrane. (From *Vertebrate Paleontology* by A. S. Romer. Copyright 1966 by the University of Chicago Press. Used with permission.)

Fig. 3 From Wiley (1981), p. 132. This figure is useful for illustrating the third criterion of identifying transformation series. See text. Reprinted by kind permission of the publisher from Wiley E.O. 1981, *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*, p. 137, New York: John Wiley & Sons. Copyright © 1981 by John Wiley & Sons, Inc

Remane’s three criteria of primary homology—topology, special quality, and series of intermediate forms—are the only ones Wiley (1981) discusses in the context of primary homology assessment. A word is in order regarding the *logical relationships* among Remane’s three criteria. Wiley (1981) holds that the three are independent, and that homologous characters need not meet all of them. Rieppel and Kearney (e.g., Rieppel 1988; Rieppel and Kearney 2002), disagree with the first claim and possibly with the second. They write:

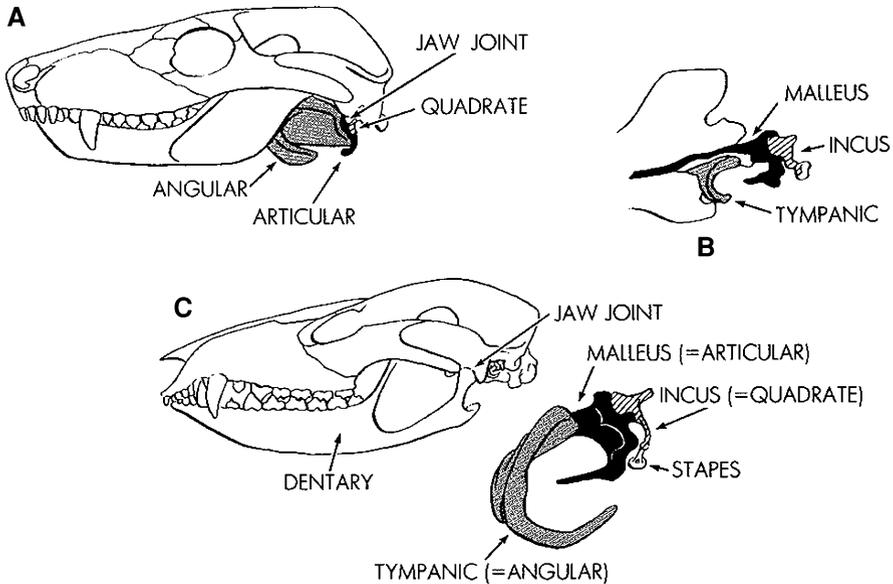


Fig. 16.2 Transformation of the mammal ear (after J. Hopson; Crompton and Parker, 1978). A, the skull and middle ear of a mammal-like reptile, *Thrinaxodon*. B, the lower jaw of an opossum fetus. C, the skull and middle ear of an adult opossum.

Fig. 4 From Radinsky (1987), p. 144. Diagram indicating the transformation of the mammalian middle ear from a mammal-like reptile. See text. Reprinted by kind permission of the publisher from Radinsky L.B. 1987, *The Evolution of Vertebrate Design*, p. 144, University of Chicago Press. Copyright © 1987 by University of Chicago Press

As was argued by Hennig (1966), the recognition of special quality of structures, as well as the recognition of intermediate forms, requires a primacy of the criterion of topological correspondence (see also Riedl 1978; Rieppel 1988), because to establish a special quality or intermediacy of a structure requires the previous recognition of the potential equivalence of the structures based on topology. (Rieppel and Kearney 2002, p. 75)

Thus, they claim that the topological criterion is logically primary. Equivalence (sameness) is initially evaluated in terms of position. This also pertains to *another* criterion that Rieppel and Kearney identify: *connectivity*. (I have chosen not to discuss connectivity as an objectivity criterion because I hold that it can be folded into the first criterion.) Now, regarding the primacy of topology, they go further and argue that even “the establishment of topological relations for a given structure requires a frame of reference which, again, can be tested in its own right.” (p. 64) In short, empirically-assessed positional equivalence is critical for the employment of Remane’s second two criteria. I will not here further adjudicate Wiley’s and Rieppel and Kearney’s arguments regarding the (in)dependence of the three criteria. However, I suggest that, ideally, these criteria should mutually inform and reinforce one another. Furthermore, if they explicitly conflict, careful investigation into the

reasons for their conflict needs to be done. Criteria 5 and 6, to be explored below, can be of much use in cases of criterial conflict.

A fourth (4) criterion for identifying primary homology is Patterson's (1982, 1988) *conjunction criterion* (see also de Pinna 1991; Rieppel and Kearney 2007, p. 96). Here is Patterson's clear prose and lovely example:

Conjunction is the name I gave to a test that will disprove homologies as "anatomical singulars," Riedl's (1978, p. 52) apt term for homologues. If two supposed homologues are found together in one organism, they cannot be homologous. For example, the theory that the human arm (a mammalian forelimb) and the wings of birds are homologous would be shown to be mistaken if angels (with both arms *and* wings) are ever discovered. (Patterson 1988, p. 605; the angel example is not in his 1982).

Thus, a given character cannot be homologous if two of its putatively mutually exclusive states are found in the *same* organism. Or, to continue with our mammalian middle ear example, if we found some derived group of teleosts that had two (or more) bones where other derived teleosts have their single hyomandibular bone (and where mammals or even squamates have their stapes), our hypothesis, our abstraction, of the homology between the hyomandibular bone and the stapes would be put into question. What would we homologize to what? Investigating development would help, but the conjunction criterion must still *also* rely on judgments, on abstractions, of topology, even in embryos. We would need to determine whether one of the two (or more) imagined bones might actually *simply be* the hyomandibular bone and stapes and, therefore, whether the homology claim could be saved. This abstraction and reasoning would require knowing a fair amount about spatial location and special similarity, even in development. Regardless of the relation to criterion (1), the conjunction criterion is a bona fide criterion for homology assessment.

The last two criteria—(5) the criterion of *causal grounding* and (6) the criterion of *inter-disciplinary communication*—have been defended in the work of Rieppel and Kearney. These criteria have not yet received the attention that they deserve. In what follows, I show their importance for our search for the objectivity of primary homology claims.

Kearney and Rieppel have identified a highly promising and robust criterion for character analysis: *the investigation of the causal structure underlying characters*. Their argument is highly consonant with my paper and the first two epigraphs. For example, in discussing a recent debate about snake origins, Rieppel and Kearney contend that "if characters are not required to have any causal grounding", then cladists are unconstrained in their delimitation of pertinent characters for the character matrix (Rieppel and Kearney 2007, p. 105). *Any* abstracted character would be acceptable. Recall the two solutions to the central problem of character analysis, outlined at the end of Sect. 2. Rieppel and Kearney (2007) adopt the second solution:

The problem with this approach ["phenetic cladistics: elegant analyses with many sources of error", "Wägele 2004, p. 109"] is that an appeal to causal relations has been buried under the logic of numbers. But biology has a long

tradition of doing much better: evaluating characters in a causal (developmental, functional) context. (p. 109)

Particularly in these times with rich genomic, developmental, physiological and even behavioral data, we have the means to choose causally grounded, biologically informative characters (e.g., Rieppel 2006a, p. 384; Rieppel and Kearney 2007; Kearney and Rieppel 2006). Of course, evaluating causal grounding “through empirical investigations of comparative anatomy, developmental biology, functional morphology and secondary structure” is a work-intensive solution. Moreover, causal grounding “is unlikely to hit bedrock” (Kearney and Rieppel 2006, p. 376). Causal analysis is an ongoing investigation.¹⁴ Rieppel and Kearney’s project of seeking causally grounded characters could be productively tied to recent work on mechanisms (e.g., Glennan 2002; Craver 2007). Causal grounding is a highly relevant and innovative criterion for primary homology assessment.

The final criterion that I will explore is a *socially epistemic* one. The criterion of inter-disciplinary communication does not directly legislate actual investigations of concrete objects (e.g., specimens). Rather, it promotes the sharing of meaningful causal and empirical information across scientific disciplines. That is, knowledge can be made increasingly robust when different sorts of data are shared, and further developed, across laboratories, communities, and fields (Longino 2002; Wimsatt 2007; Leonelli 2008). Moreover, inter-disciplinary communication allows for communal critique. Sharing and critique are the two sides of the same dialogical coin. Indeed, “homology and phylogeny” inferences are bolstered when they are carried out in an inter-disciplinary manner: “such explorations [“the inference of homology and phylogeny”] may be pursued in a variety of empirical research programs, such as evolutionary developmental biology, comparative morphology, ontogenetic studies, and genetics”. (Kearney and Rieppel 2006, p. 376) The key, then, is for information to subsequently flow and be critiqued across communal and disciplinary boundaries. Objective characters can be identified if our biology is comparative not just in the sense of contrasting *taxa*, but also in the sense of comparing and integrating *disciplines*¹⁵ (Table 2).

¹⁴ This is also the case for molecular characters. These also receive biological meaning from investigations into the causal reasons (in historically-conditioned genetic systems) for sequence similarity.

¹⁵ Note that this criterion is pragmatic as well as epistemic, *sensu stricto*. That is, it concerns both (1) the practices of discovering and developing primary homology claims, as well as the use and usefulness of such claims (*pragmatic*), and (2) the truth of primary homology assertions [i.e., the truth relation between character claims and the (potentially co-constructed) world] (*epistemic*). (On epistemic versus pragmatic virtues, see, e.g., van Fraassen 1980.) That this criterion is pragmatic should be evident (Sober, personal communication). But I argue that it is *also* epistemic. Consider the following gross idealization of the practice of character analysis: each phylogenetically-relevant discipline produces its own list of characters. For instance, comparative morphology, molecular genetics, and developmental biology have different “partitioning frames” (Winther 2006c) and each therefore articulates a different list. Given these lists, inter-disciplinary communication has at least two aims. First, it attempts to find the characters that are shared across disciplinary contexts. It thereby produces a collated list of strongly empirically adequate characters—i.e., of *robust* characters. Since the empirical adequacy of a shared character is bolstered through inter-disciplinary communication, this criterion has epistemic weight. Second, communication aims to identify the empirical relations among characters that are *not* shared across contexts (e.g., causal or common-cause relations). Discovering relations among non-shared characters also increases the empirical adequacy of the *total* inter-disciplinary list of characters. Again, inter-disciplinary communication is epistemically relevant.

Table 2 Table summarizing the six objectivity criteria for primary homology assessment, together with important characteristics of each

Primary homology criteria	Who first discussed it in detail?	Related to similarity?	Empirical, causal, or “meta-empirical”?
1. Topological	Remane/Hennig, Wiley	Yes	Empirical
2. Special similarity	Remane/Hennig, Wiley	Yes	Empirical
3. Series of intermediate forms	Remane/Hennig, Wiley	Yes	Empirical
4. Conjunction	Patterson	Yes	Empirical
5. Causal grounding	Rieppel and Kearney	Yes, but “deeper”	Empirical/causal
6. Inter-disciplinary communication	Rieppel and Kearney	No	Meta-empirical

Conjunction is only implicitly related to similarity in so far as we have to assess each of the two parts/characters present in the same species/taxon as homologous to each of the respective part/character in one (of two) other species/taxa. Regarding the distinction between empirical and causal, the former is intended in a purely observational sense, the latter in an ontic, fundamental sense as producing or explaining the observed parts/characters

The six objectivity criteria for primary homology claims identified in this section are what allow us to both produce and justify primary homology claims. The criteria are not water-tight. And while they ideally mutually reinforce one another, they (especially criteria 1–4) can sometimes enter into conflict. For such cases, a deeper causal analysis (criterion 5) as well as communal discussion and criticism (criterion 6) are essential. As we shall see in the conclusion, criteria 5 and 6 play special roles by integrating and giving meaning to the others. Criterion 5 justifies and explains similarity; criterion 6 provides means to fine-tune and coordinate the other five. In general, this set of criteria provide powerful guidelines—heuristics and norms—for proper character analysis.

6 Objectivity: Causal Analysis and Dialogue

I conclude with the philosophical themes of subjectivity and objectivity in scientific knowledge. In particular, I contrast my account with Richard Richards’ philosophical investigations (2002, 2003). Richards is perhaps the only philosopher who has been occupied with the difficulties of character analysis in cladistics. Although there is much to admire in Richards’ project, my concern is to show that the criteria need not be entirely subjective. Under my proposal, shared and explicit criteria of character analysis aim to be *objective*, both in general and in particular implementations. First, as general criteria they achieve a fair amount of objectivity precisely because their justifying-power is discussed and tested publically. By viewing this case through a sophisticated communitarian empiricist epistemology (e.g., Longino 1995, 2002; Kusch 2002) we avoid falling prey to the “mob psychology” charge of which Lakatos accused Kuhn, and which Richards suggests that critics of cladistic analysis can accuse those individuals or research groups who insist on particular sorts of theory-laden character and not others (Richards 2002). Second, as criteria implemented in particular cladistic studies, the criteria attain

objectivity both from what they inherit from public discussion and from guiding an abstraction process that (1) interacts with actual specimens (objects) and their properties and (2) identifies causal structure that grounds and explains character ascriptions. Thus, although there is strong reason to be concerned with the subjectivity of character analysis and of the resulting cladograms (Richards' argument), I have argued that we do have means of separating true from reified characters and hence of attaining some objectivity in cladistic inference.

Let us explore Richards' argument in more detail. He expresses concern with the "indeterminacy" and "subjectivity" of character individuation (Richards 2003). He writes:

What is important here is that there is no algorithm for the formulation of the data set—no algorithm to determine which characters to include in parsimony considerations. Instead, background information about development, character change and evolutionary processes seems to influence the choice of characters. But also of particular interest here, tradition and training seem to play a role. (Richards 2002, p. 15)

According to Richards, there is no "algorithm" or rule with which to individuate characters. Moreover, "background information" is opposed to "algorithm"—these are taken to be mutually exclusive. Finally, "tradition and training" are emphasized as a source of character ascriptions, a source that Richards takes to be subjective and also in opposition to algorithmic rules. Thus, Richards constructs a stark contrast between algorithmic choice, on the one hand, and decisions based on background information and tradition as well as training, on the other. He goes even further in his other paper on the topic:

Which hypothesis we accept as the best phylogenetic hypothesis depends on how we individuate characters. But if we have no satisfactory grounds for preferring one character individuation scheme over another, it is unclear why we should regard our evaluation of phylogenetic hypotheses as anything more than a reflection of our predispositions or biases. The outcome of phylogenetic inference therefore seems as much a consequence of illegitimate nonscientific factors as it is a consequence of legitimate scientific factors. (Richards 2003, p. 277)

Richards is now contrasting "scientific" with "nonscientific" factors. Although the relation between "predispositions or biases" and "factors" is not clear, one plausible way to read Richards is to see him as characterizing background information, tradition, and training as "sociological" (pp. 277–278) factors that are the source of our *nonscientific* "predispositions and biases." Again, we are presented with a strong contrast between scientific algorithms and non-scientific background information, tradition, and training.

Contra Richards, I have in effect argued that we should not draw such sharp lines. It is evident that we employ predispositions and biases, i.e., theory, in the character individuation process. But this does not make the characters we identify illegitimate or "non-scientific". The use of biases and heuristics is inevitable and not pernicious, as long as we subject the abstraction process and its products to the six objectivity

criteria for character assessment described in Sect. 5. In this context, it is also important to observe that experts have deep insight *precisely because* they appropriately manage to combine a variety of knowledge-producing factors: background information, tradition, training, operational methods, and ontological assumptions. Is this non-scientific? Again, I caution against distinguishing scientific from non-scientific factors too starkly, and from claiming that character individuation is subjective simply because it does not follow a single, rigid “algorithmic” procedure.¹⁶

In concluding this paper, I would like to briefly indicate how the last two criteria are of particular importance in the search for objectivity. This also provides a response to Richards’ worries.

Causal grounding is crucial because it provides a way to justify our similarity claims. While the first four criteria provide excellent reasons for identifying, individuating, and measuring characters, the fifth criterion in effect explains why they work so well. That is, similarity is explained by the sharing of causal genetic, developmental, and even physiological mechanisms across taxa. This sharing of causal mechanisms is due to common ancestry and to developmental constraints that can limit further changes of the mechanisms in related clades (e.g., Rieppel 1994, 2005; Wagner 1994, 1996; Winther 2001). In short, *sameness of (potentially phylogenetically-constrained) cause explains sameness of characters*.

Both Wagner and Rieppel have located a philosophical account congenial to this biological argument in the work of Quine and Putnam. As Wagner points out, Quine “suggested that natural kinds can only be defined in the context of a process or a theory of a process in which these entities act as a unit.” (Wagner 1996, p. 36). Quine argued that a similarity approach to characterizing kinds would, with the advance of “theoretical science”, be replaced by theories that “reveal hidden mysteries, predict successfully, and work technological wonders” (Quine 1977, p. 170).¹⁷ That is, “things are similar in the... theoretical sense to the degree that they are interchangeable parts of the cosmic machine revealed by science” (p. 171). Thus, we explain similarity measures by uncovering the “parts of the cosmic machine.” Similarity is accounted for by causal grounding.

Now, in his analysis of “the description of meaning”, Putnam differentiates among four components of the meaning of a natural kind term: syntactic markers, semantic markers, stereotype, and extension (Putnam 1996 (1975), pp. 48–49). The details are complex, but can be adapted for our purposes. In identifying and individuating characters, a competent speaker/cladist first introduces a potential character-term indexically, by ostension—certain sorts of objects or processes are

¹⁶ Although I cannot argue for this further here, the indeterminacy and the under determination of rule application is a generalized worry relevant to all of science. Despite indeterminacy and under determination—explored by Quine, Goodman, and “Kripkenstein”, as well as other philosophers—scientists productively employ rules, heuristics, and methodology that allow science to progress. This suggests that the *strong* skepticism about rule application and rule existence entertained by Richards is unwarranted.

¹⁷ It is important to note that Quine was a thoroughgoing empiricist and naturalist. That is, he was skeptical about the analytical role, even coherence, of notions like “cause”, “disposition” or “the real”. And yet, he felt that science was progressing—its inductions were to a large extent successful. I will not delve further into important and finer points of Quine scholarship.

picked out by a stereotype (i.e., the properties of a typical, exemplary type of object or process, e.g., “colorless, transparent, tasteless” in the case of “water”, p. 49). For example, “vertebral column” has certain stereotypical properties that initially allowed us, as scientists, to pick out particular objects (and not others) as vertebral columns (see Rieppel and Kearney 2007, p. 101). Note that the stereotype defines the kind. The stereotype is also a sort of similarity measure. Now, as science advances, it explores the causal grounding of the stereotype and finds that the stereotype can be accounted for by a causal microstructure. This is the actual extension (e.g., H₂O as such). Thus, again, a similarity measure is accounted for by causal grounding.¹⁸ Thus, as Wagner and Rieppel argue, Quine’s and Putnam’s accounts of natural kind terms can be used to show how the fifth criterion philosophically justifies the other four.

Let us turn to the last criterion. Inter-disciplinary communication is crucial for a variety of reasons. It facilitates the sharing of data, theories, methodologies, and standards. It also opens up multiple avenues and audiences for criticism. This criticism further strengthens the data, theories, methodologies and standards (e.g., Popper 1963). In contemporary philosophy of science, there is an increasingly powerful and, I believe, correct move to emphasize the inherently social nature of epistemically-tested knowledge. Indeed, a socially-organized complex science need not be seen as conflicting with a science seeking objective empirical knowledge.

Feminist philosophers of science have been particularly good at developing this point. For instance, in an insightful analysis of a variety of meanings of “objective”, Lloyd (1995, p. 373) argues that “the concept [of objectivity] is community-based or socially-grounded in its significance to knowledge and truth”, citing important epistemologists who also argue this point (e.g., Carnap, McDowell and Thomas Nagel). Furthermore, in her book, *The Fate of Knowledge* (2002), Longino develops a sophisticated account of the “social character of...[the] cognitive, or knowledge-productive, capacities [of “scientific inquiry”]” (p. 8). Her account is a “socialized (not *sociologized*) account of knowledge” (p. 124) in which “epistemically acceptable” data has to be considered in the context of:

reasoning and background assumptions which have survived critical scrutiny from as many perspectives as are available [to the “community”]... and [the community] is characterized by venues for criticism, uptake of criticism, public standards, and tempered equality of intellectual authority (p. 135).

Knowledge, under Longino’s account, requires *evidence* that conforms to the world in an *epistemically acceptable* manner. Under her account, “mob psychology” dissolves and becomes transformed to constructive communally-distributed sharing of information *and* avenues for criticism. Longino’s analysis is pertinent because the other five objectivity criteria of character analysis are themselves the product of sharing and criticism. They have become public standards for the

¹⁸ Richard Boyd (1999) also has an account of how natural kinds can be grounded causally (mechanistically). Although his “homeostatic property cluster kind” account differs radically with Quine and Putnam with respect to both the semantic tightness of the intension, and the uniformity of the extension, of natural kind terms, he shares their view that (a broader) similarity of the extension of objects or processes of natural kinds should be explained by a causal (mechanistic) account.

evaluation of the characters of biological objects and processes. (They are also objective because they legislate appropriate interaction with real objects and processes. See also Harding 1995.) The criteria are of course subject to further refinement and my list is neither absolute nor final. As Otto Neurath pointed out, we are constantly rebuilding the ship of science at sea, and the objectivity criteria of character analysis continue to be subject to ongoing dialogue and empirical test.

Although the role of causal grounding and inter-disciplinary communication as criteria that make character abstraction and character analysis *objective* needs to be further elaborated, I have tried to argue that we need not accept Richards' overly pessimistic, subjectivist view of character analysis. The dangers of reification are widespread in our biological sciences, sciences for which abstraction is so essential (for a variety of analyses on abstraction and reification in biology, see Levins 1966, 2006; Levins and Lewontin 1985; Lewontin and Levins 2007; Winther 2006a, b, 2008). In conclusion, our contrast in cladistics should not be one between really real characters and purely "abstracted" characters, as Richards argues both explicitly and with his distinction between "scientific" and "nonscientific" factors. Why not? Well, because all good characters are *both* real and abstracted. Instead, our contrast should be between theory-laden, robustly real characters *and* uncritically reified ones. Since abstraction and theory (epistemology) is invariably involved in character analysis, we can never appeal or have access to a First Metaphysics. However, as a community of systematists, we do have recourse to socially and empirically evaluated objectivity criteria, which permit us to distinguish robustly real from irresponsibly reified characters and, thereby, do our cladistic inference correctly.

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