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The Character Individuation Problem: A Philosophical Study of the Individuation of

Characters in Biological Taxonomy

by

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ABSTRACT

Biological characters are the data taxonomists use to determine evolutionary relationships among taxa. Since the number of common characters is determined by how these characters are individuated, the individuation of characters determines the selection of hypotheses about the order of evolutionary events. Richards (2003) suggests that without the use of a principle for individuating characters that is immune to personal perspective or bias, hypotheses about the order of evolutionary events may be selected subjectively. Winther (2009) responds by explaining that character abstraction, which is prior to individuation, is necessarily theory-laden rather than biased. In this thesis, I discuss the failings of these accounts and then offer some suggestions concerning how to better approach the character individuation problem.

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Chapter One: Introduction

Biological characters like 'has mammary glands,' 'has three middle-ear bones,' and 'has hair' are the data taxonomists use to determine that taxa like humans and cats are more closely related to one another than they are to lizards. Taxonomists, then, hypothesize the order of evolutionary events with the goal of eventually reconstructing all of evolutionary history. Selection of each hypothesis is determined by the number of characters two taxa have in common relative to a third. Humans and cats are more closely related to one another than either of them is to lizards if humans and cats have more common characters than humans and lizards or cats and lizards do.¹ Since the number of common characters is partially determined by whether features like 'has three middle-ear bones' are individuated singly or as multiple characters, the individuation of characters determines the selection of hypotheses describing the order of evolutionary events.

While biologists have been discussing the individuation of characters for quite some time, in 2003 the first philosophical work devoted entirely to a sustained analysis of the character individuation problem was published. Richard Richards (2003) suggested that without the use of a principle for individuating characters that was immune to personal perspective or bias, hypotheses about the order of evolutionary events may be selected subjectively; there would be nothing stopping a taxonomist from defending their preferred hypothesis with an array of characters individuated specifically to support that

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hypothesis. After discussing several principles of individuation, Richards (2003) concluded that biologists have no way of individuating characters that is immune to bias; he suggested that, as a result, biologists and philosophers would need to entirely rethink the concept of characters.

In 2009, Rasmus Winther responded to Richards' (2003) conclusion that biologists lack a bias-free principle for individuating characters; he explained that character abstraction, a process of character selection prior to individuation, is necessarily theory-laden rather than biased. Winther (2009) suggested a set of six criteria which would ensure that only the characters established to be homologous (rather than homoplastic)² by rigorous empirical testing would be abstracted. A character is homologous if it is the same character in multiple instances; each instance may vary from the others but it is nevertheless the same character. Since homologues are the heritable variation required for evolution, Winther (2009) considers them to be the real characters of the evolutionary past. Restricting abstraction of characters to homologue abstraction, for Winther (2009), solves the character problem before individuation occurs because then only the characters of the evolutionary past are being used to reconstruct evolutionary history.

With this goal of reconstructing evolutionary history in mind, Chapter Two provides a discussion of taxonomic methods, how characters determine taxonomic hypotheses, and how the character individuation problem arises as a result. In Chapter

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¹ "Common" characters here are ideally derived homologues, the same characters with varying instances among taxa but a unique variation shared by the group in question (humans and cats in this example).

Three I discuss Richards' (2003) approach to the character individuation problem as well as problems with his approach which undermine his pessimistic conclusions. Chapter Four discusses Winther's (2009) optimistic approach to the problem, compares it to Richards' (2003) view, and explains why his six criteria do not provide a solution to the character individuation problem. Finally, in Chapter Five, I review the character individuation problem and discuss two important points brought to light by my analysis of Richards (2003) and Winther (2009): the need for an unequivocal principle of character individuation, and the need for context to be taken into account when individuating characters. While I do not present a solution to the character individuation problem, I do offer suggestions for future investigations.

² Homologous characters are shared characters with varied instances among taxa while homoplastic characters are different characters with similar instances among taxa.

Chapter Two: Taxonomy and the Character Individuation Problem

The biological classification of organisms has been the subject of debate in both biology and philosophy since long before the two were separate disciplines. Two major topics concerning biological classification which have been debated by biologists in great depth for quite some time are what a species is, and what homology is. The species question was first to catch the attention of philosophers of biology, and more recently homology has been recognised as being a philosophical problem. Similarly, characters have been a topic of hot debate in biology for a number of years and philosophers have begun to take notice. ³

2.1 Evolutionary History, Taxonomy, and Phylogenetic Inference

Classification of organisms is extremely important to many biological subdisciplines. It is so important that one biological sub discipline, taxonomy, is devoted entirely to the provision of methods and sorting principles for classification of organisms (Ereshefsky 2001, 51). Taxonomists, as their name suggests, sort organisms into groups called taxa and sort those taxa into more inclusive taxonomic groups (Ereshefsky 2001, 51). Four schools of taxonomy have evolved since the "modern synthesis"—the integration of Mendelian genetics with Darwinian evolutionary theory in the first half of

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³ Homologues are the same parts or properties in various species while *characters* are those parts or properties used as data for classification of species. While some taxonomic schools ideally use only homologous characters, these schools actually individuate characters which correspond to homologues; it is not the homologues themselves which make-up the data set, but their corresponding characters. Characters and character individuation are discussed in sections 2.2 and 2.3 respectively.

the twentieth century (Ereshefsky 2001, 52). While they each have a different methodology and different reasons for preferring their own methods and principles to those of the other schools, all four schools of taxonomy use the characters of organisms to classify them.

Evolutionary taxonomy, the school developed in conjunction with the "modern synthesis", classifies organisms by recency of common ancestry as well as significance of evolutionary change (Ereshefsky 2001). This type of classification groups taxa using homologous characters. Homologous characters can be roughly defined as being the same trait by virtue of common ancestry, the instances of which may differ by form or function. Evolutionary taxonomists sort organisms into taxa by tracking the number and extent of variation in homologous characters. Process cladists, members of a taxonomic school which I discuss in greater detail later, also use the number of homologous character variations to form their classifications but reject using information about the extent of variation among such characters.

Pheneticists use characters to construct classifications as well, but are opposed to basing taxonomic classification on a single type of character as the other three schools do (Ereshefsky 2001, 60). Pheneticists classify organisms according to overall similarity. By recording as many characters as possible with no restrictions or preferences for types of characters, they group taxa by the greatest overall number of shared characters (Ereshefsky 2001, 61). Proponents of this taxonomic school argue that their method of classification is theory free and timeless, thus preferring it to those which make theoretical assumptions about characters (Ereshefsky 2001, 60). This preference stems from a desire to retain maximum objectivity in biological science and the supposition that theoretical assumptions will lead to subjective classifications.

Pattern cladists, proponents of one of two cladistic taxonomic schools, and pheneticists share both the desire for objectivity and the supposition that theoretical assumptions lead to subjective classifications. Pattern cladists, however, use only one type of homologous character to produce their taxonomic classifications while pheneticists consider such restrictions to be based on theoretical assumptions. Pattern cladists argue that they can classify organisms using "defining characters" which are not theoretically linked to assumptions about particular evolutionary processes (Ereshefsky 2001, 76). This rejection of genealogical classifications of taxa is supposed to allow classification patterns to be independent from, while still compatible with, evolutionary theory (Ereshefsky 2001, 78).

Process cladism and pattern cladism share the methods and principles which I discuss below with the important exception that process cladism is based on the view that taxonomic classifications are representations of branching events in evolutionary history while pattern cladists take them to be branching patterns and nothing more (Ereshefsky 2001). For process cladists, each taxon has an evolutionary history which is causally related with the evolutionary history of many other taxa (Ereshefsky 2001, 66-67). As populations of organisms change and evolve over time, speciation events occur in which single populations split into two distinct populations, each forming a new taxon; these events are seen by process cladists as the branching of taxonomic lineages (Ereshefsky 2001). The evolutionary history of a taxon, including all of its ancestor-descendent relations with other taxa, is called its phylogeny (Freeman and Herron 2004, 549). A

phylogenetic tree is a graphical representation of a phylogenetic hypothesis, including information about the relationships among taxa, the order of evolutionary events, and the rates of evolutionary change (Ereshefsky 2001, 71; Freeman and Herron 2004, 549).

Since evolutionary history cannot be observed directly, phylogenies must be inferred from characters, as with the taxonomic classifications produced by the other three schools (Ereshefsky 2001; Freeman and Herron 2004, 549). Process cladists infer phylogenies by first producing cladograms (Ereshefsky 2001, 71). For a process cladist, a cladogram is a graphical representation of relationships among the taxa under study, grouping taxa by the recency of their common ancestors. Taxa are "grouped together when they originate in the same branching event," when they "share a more recent common ancestor than either shares with a third taxon." (Ereshefsky 2001, 67) Two taxa which are grouped this way are referred to as sister taxa (Ridley 1993). In Figure 2-1, for example, taxon A and taxon B are sister taxa; they are more closely related to each other than either is to taxon C. Similarly, the taxonomic group containing taxon A and taxon B (let us call it AB) is a sister taxon to C; AB and C are more closely related to one another than either is to D.



Figure 2-1 A cladogram showing the relationships of taxa A-E

Once a cladogram showing the relations among taxa has been produced, the method of which we will discuss shortly, a phylogenetic tree can be inferred by adding information about known ancestral relations. This is referred to as "rooting" the tree, the most common method of which is outgroup comparison (Ridley 1993, 460). Outgroup comparison involves adding a taxon to the analysis that is known to be closely related to but "phylogenetically outside" the group of taxa under study (Ridley 1993, 460).



Figure 2-2 A hypothetical phylogenetic tree showing the ancestral relationships of snakes A-E using lizard F as an outgroup taxon

For our cladogram showing the relations among taxa A-E, we would add taxon F, a group of organisms shown by a previous evolutionary study to be closely related to, but outside, the group of taxa we are studying. Once we have selected F, we would determine the state of its characters and set those states as being the ancestral states. If taxa A-E are all snakes in our example, F could be a closely related lizard which is found earlier in the fossil record than all the snakes under study. Using this outgroup, having complete limbs could be the ancestral state of the limb character, so the phylogenetic tree corresponding to our cladogram would show all the snakes with incomplete or rudimentary limbs as sharing a derived character. Similarly, some standard thickness could be the ancestral state of the rib character such that any snakes with thickened ribs would be shown to share a derived character. The individuation of such characters and their possible states will be discussed in section 2.3.

Figure 2-2 shows a hypothetical phylogenetic tree rooted by F that corresponds with the cladogram from Figure 2-1. The primary difference between a phylogenetic tree and a cladogram is that the cladogram only asserts the closeness of relations among taxa relative to the other taxa under study; the phylogenetic tree, on the other hand, also asserts the existence of such groups and that the relations among the taxa included imply ancestor-descendent relations (Sober 1988, 22). The principle that allows for the transition from cladogram to phylogenetic tree is the same principle the process cladists use to construct their cladograms in the first place: the parsimony principle (Ridley 1993, 460).

Parsimony assumes that evolutionary change is improbable such that if an ancestor and its descendent share a particular character it is more probable that all intermediate taxa also share that character than it is that an evolutionary change and a reversal of that change both occurred (Ridley 1993, 449). For any set of taxa, "a phylogeny requiring less evolutionary change is more plausible than one requiring more." (Ridley 1993, 450) For this reason the use of parsimony in phylogenetic inference minimizes the number of evolutionary changes assumed in the production and selection

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of cladograms and phylogenetic trees (Ereshefsky 2001, 73; Freeman and Herron 2004, 554; Ridley 1993, 449).

When parsimony is used for the initial selection of one cladogram over others, it is the cladogram with the fewest total character changes that is taken to be the correct representation of relative closeness for the group of taxa in question. 'Character changes' here are changes from one character state to another. We will discuss characters and their states further in section 2.3 when we discuss individuation of characters. For now, however, let us assume that each character can have only two states, the state '0' or the state '1'. In our sample cladogram above we suggested that a 'limb' character may be in either a 'complete' or 'incomplete' state. If having complete limbs is coded by '0' and having incomplete limbs is coded by '1' then our 'limb' character can be coded as '0' or '1' for each species under study. If taxon A has complete limbs, then A is coded as '0' for the 'limb' character. Similarly, if taxa B and C have incomplete limbs, then B and C are coded as '1' for the 'limb' character. We can do the same state coding for each character of taxa A, B, and C. Imagine that A, B, and C can each be coded for ten characters, q, r, s, t, u, v, w, x, y, z, and we have coded the states of each of these characters into Table 2-1.

	A	B	C
<i>q</i> , r	1	0	0
s, t, u	1	1	0
v, w, x, y, z	0	1	1

Table 2-1 Character Data for Taxa A, B, and C

Once we have coded states for all the characters shared⁴ by taxa A, B, and C, we can use parsimony to determine the relative closeness of relation among these taxa. We will use the character data in Table 2-1 to determine whether taxa B and C are more closely related to each other than either is to A (Figure 2-3a), A and B are more closely related to each other than either is to C (Figure 2-3b), or A and C are more closely related to each other than either is to B (Figure 2-3c). In order to determine which is the most parsimonious hypothesis, we must first determine how many evolutionary changes are posited by each hypothesis.



Figure 2-3 Three cladograms showing relations among taxa A, B, and C including the transition from state 0 to state 1 of characters q, r, s, t, u, v, w, x, y, and z

⁴ 'Shared' characters here refers to homologous characters, the same character with a different form or function (a different character state). We will discuss this in further detail in section 2.3.

Any change from one character state to another counts as a single evolutionary change. For example, of the ten characters coded for taxa A and B, only three have the same state in both taxon A and taxon B (namely s, t, and u). So when a cladogram hypothesizes that A and B share a branch (as Figure 2-3b does), this hypothesis posits a state change in the remaining seven characters within that branch. Characters q and rchanged from 0 to 1 somewhere on the way to A from the branching point AB while characters v, w, x, y, and z changed from 0 to 1 somewhere on the way to B from the branching point AB (labelled in Figure 2.3b). In this way we can determine that the branch AB represents seven evolutionary changes. The same method can be used to determine the character changes posited in the rest of cladogram b (Figure 2-3). The three characters with the same state for all of branch AB (s, t, and u) changed from 0 to 1 somewhere on the way to branching point AB while the characters v, w, x, y, and z changed from 0 to 1 somewhere on the way to C. If we add the seven evolutionary changes posited by the branch AB to these eight evolutionary changes posited by the hypothesis that C is closely related to the branch AB, we have determined that the cladogram b in Figure 2-3 represents a total of fifteen evolutionary changes.

Using the same procedure as described above, we can count the number of evolutionary changes posited by each of the other two hypothesized cladograms. I have, however, labelled the state changes for each of the characters on the cladograms so that the evolutionary changes posited by each cladogram can be easily observed and counted. Cladogram a in Figure 2-3 posits thirteen evolutionary changes while cladogram c in Figure 2-3 posits eighteen changes. Since cladogram a posits thirteen changes, b posits fifteen changes, and c posits eighteen changes, the cladogram which posits the fewest evolutionary changes is cladogram *a*. Cladogram *a*, then, is the most parsimonious hypothesis because it posits fewer evolutionary changes than the other two possibilities.

Similarly, when a cladogram is rooted using the addition of an outgroup taxon, the selection of an outgroup and the assumption that the character states of that taxon are ancestral, are applications of the parsimony principle. Since it is more likely that a character state shared by an ancestor and its descendent was also present in all intermediate taxa, those character states exhibited by a closely related taxon predating all the taxa under study are those most likely to be ancestral. To return to our snake example from earlier in this section, the hypothetical outgroup to taxa A-E, F, is closely related to but phylogenetically outside our taxonomic group of interest. For this reason it is more parsimonious to assume that the character states which F exhibits were also exhibited by the common ancestor of F and our group of interest. These character states, then, must represent the starting states from which we count the number of changes represented by our inferred phylogenetic tree. So the tree entailing the least number of changes, as with our selected cladogram, is the most parsimonious inference for the group of taxa we are interested in.

The parsimony principle and the methods outlined above allow cladists to produce taxonomic classifications from the characters exhibited by the taxa they study. The other two taxonomic schools (pheneticism and evolutionary taxonomy) use different sets of methods and principles, but as discussed earlier in this section, all of their methods and principles also result in the production of classifications from character data. Although the methodology and general types of characters used vary for each of the four schools, it will become clear by the end of this chapter that the problem with which I am concerned is a problem for all taxonomists regardless of the methods, principles, and general types of characters used to produce their classifications. That being said, I will primarily focus on process cladism during my development and discussion of what I call the "character individuation problem" in order to make evident that the problem is a problem regardless of which school one prefers.

2.2 Characters: The Taxonomic Data

Characters are the taxonomic data used by cladists to infer phylogenetic relationships among taxa. Minimally, a character is a "heritable, organismal feature (i.e. an observable condition) expressed as an independent variable." (Sereno 2007, 570) In order for a character to be of interest to cladists, however, it must express a particular type of trait shared by two or more taxa, a derived homology (Freeman and Herron 2004, 550-560; Ridley 1993, 452). Cladists divide shared traits into three categories: analogues, ancestral homologues, and derived homologues (Ridley 1993, 451).

> If it was present in the common ancestor of the two species, it is a homology; if it was not (and therefore evolved convergently) it is an analogy. Homologies, in turn, divide into ancestral and derived homologies. An ancestral homology was present in the common ancestor of the two species, but evolved earlier and is also shared with other, more distantly related species; a derived homology first evolved in the common ancestor of the two species and is not shared with other more distantly related species. (Ridley 1993, 451-452)

Consider the characters a and a' in the cladogram showing the relationships among taxa A-E (Figure 2-4). Since the character shared by taxa A and B, a', is also present in their common ancestor, it is a *derived homology* of A and B. The character shared by taxa D

and C, a, is not only present in their common ancestor but is also present in the ancestor they both share with taxon E, a more distantly related taxa; so a is an *ancestral homologue* of taxa D and C. While a' is present in both taxon E and taxon A, it is not present in their common ancestor, suggesting that the trait evolved separately in each taxon; so a' is an *analogue* of taxon E and taxon A.



Figure 2-4 A cladogram showing ancestral relationships among taxa A-E

Cladists and evolutionary taxonomists emphasize the need for characters to have historical continuity (Wiley 1981, 116). E.O. Wiley's (1981, 116) definition of character makes evident his desire to underline the sequential continuity resulting from the heritability of characters:

> A character is a feature of an organism which is the product of an ontogenetic or cytogenetic sequence of previously existing features, or a feature of a previously existing parental organism(s). Such features arise in evolution by modification of a previously existing ontogenetic or cytogenetic or molecular sequence (Wiley 1981, 116).

So, for Wiley (1981), a character is any feature of an organism which is the heritable product of the organism's development (ontogeny), cellular structure (cytogeny), or molecular structure. Homologues, characters shared by two species and their common ancestor(s), have just the sequential continuity that Wiley (1981) demanded of characters.

The type of shared characters that cladists are interested in, however, are derived homologues because only derived homologues provide evidence for recency of common ancestry (Freeman and Herron 2004, 550; Ridley 1993, 452). These shared characters have historical continuity with the ancestral homologues but represent a change, the modification component of Darwin's 'decent with modification'. Such characters may be morphological, molecular, genetic, mechanistic, or behavioural as long as their homology relation and novelty can be established (Freeman and Herron 2004, 550; Gilbert and Bolker 2001; Ridley 1993, 466; Wainwright and Friel 2001; Wheeler 2001, 309).

A second criterion for characters, as Sereno's (2007) minimal definition of character emphases, is that taxonomic characters be independent of one another (Freeman and Herron 2004, 550; Sereno 2007, 569)

Independence means that if a character undergoes a change in the course of evolution, then that change cannot induce a change in another character. With molecular data, for example, researchers have to be able to defend the claim that a change in a particular base in a DNA sequence does not cause a correlated change in another base being studied. (Freeman and Herron 2004, 550)

The problem that arises when individual characters are causally related is that a single evolutionary change is represented as multiple changes. As discussed in the previous section, selection of the best (most parsimonious) inference for each data set is based on the number of evolutionary changes each potential inference assumes. If characters lack independence, the use of parsimony for selection of the best inference is invalidated (Freeman and Herron 2004, 550).

There is abundant debate about further stipulations on characters and more specific definitions of characters for use in phylogenetic inference but what seems to be agreed upon is the need for taxonomic characters to express causally independent novelties of homologous features (Freeman and Herron 2004; Ridley 1993; Sereno 2007). Simply put, the independence criterion for characters ensures that evolutionary changes are only counted once, while the homology requirement ensures that the characters compared during phylogenetic analyses are the same characters and thus actually comparable. These criteria are applied during the individuation of characters, the process of which is the topic of the next section.

2.3 Character Individuation: Characters, Character States, and Character Sets

As discussed in the previous section, a *character* can be minimally defined "as a heritable, organismal feature (i.e., an observable condition) expressed as an independent variable" (Sereno 2007, 570); characters are the data used for phylogenetic inference. For this reason, it is important to consider how such data is 'collected', or more appropriately, 'individuated'. Individuation of characters involves picking out comparable (homologous) characters and recording the differences in their form, function, location, etc. by assigning a character state to each instance. If one were comparing snakes to lizards, for example, one of the characters individuated could be the 'vertebrae number' with states 'less than 100', 'between 100 and 300', and 'greater than 300'.

A character state is a "mutually exclusive condition of a character" (Sereno 2007, 570). 'Mutually exclusive' suggests that if 'less than 300' is one of the states for some character, 'greater than 200' cannot be a state of the same character. For each character, only one character state may apply to any organism (real or hypothetical). Since it is logically possible for an organism to have both 'greater than 200' and 'less than 300' vertebrae, these cannot both be character states for the 'vertebrae number' character. This rule about the character states for any single character being mutually exclusive from one another pertains to that character and its states within a single phylogenetic analysis. The example above used the states 'less than 100', 'between 100 and 300', and 'greater than 300' as character states of the character 'vertebrae number'. In a phylogenetic comparison of several snakes, the states for the 'vertebrae number' character may be 'less than 325', 'between 325 and 350', and 'greater than 350'. While the mutually exclusive states criterion would not allow 'greater than 300' as a character state in this phylogenetic comparison, it remains a viable character state for the same character in our original analysis.

As discussed above, the characters and character states for an organism may vary depending on the phylogenetic study. If only some of the organisms in the study have vertebrae, for example, our 'vertebrae number' character from the lizard-snake comparison would not be included because not every organism in the study would have a state for that character. Rather, we might have 'vertebrae' as a character with 'present' and 'absent' as possible character states. Sober (1988, 35) notes that the "distinction between character and character state is relative to the phylogenetic level of analysis." The example he uses to illustrate is behavioural; 'walking' may be a character state for

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the 'form of locomotion' character in an analysis including humans and fish while the 'walking' character has states 'upright' and 'non-upright' in a comparison of primates (Sober 1988, 35).

I refer to the set of all characters and their states as they have been individuated for a single organism in question as that organism's *character set*. In our snake-lizard example above, the character set for snakes would include the character 'vertebrae number' with the state 'greater than 300' while the character set for lizards may include the character 'vertebrae number' with the state 'less than 100'. A character individuation is the set of character sets for those organisms included in a single phylogenetic analysis. So the character individuation for our snake-lizard example would include the 'vertebrae number' character with 'greater than 300' as the state for snakes and 'less than 100' as the state for lizards. While the third state 'between 100 and 300' vertebrae, might not be part of any organism's character set, it would remain part of the character individuation as a state which some hypothetical organism could have for the 'vertebrae number' character. To avoid confusion, I refer to the active parsing of organisms into their respective character sets as *individuation of characters* rather than *character* individuation. It should be kept in mind, however, that the same is not done by others who write on this topic.

2.4 Character Individuation: Examples

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In section 2.2 I discussed the differences between derived and ancestral homologues. Recall that derived homologues are characters shared by two species and their most recent common ancestor; "a derived homology first evolved in the common

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ancestor of the two species and is not shared with other more distantly related species." (Ridley 1993, 452) Having three ear ossicles (auditory bones) rather than only one ear ossicle is a derived homologue of mammals,⁵ for example (Ax 1987, 144). This means that the most recent common ancestor of platypus and humans—Monotremata and Placentalia—shares the character state 'three' for the character 'number of ear ossicles' with platypus and humans (Figure 2-5). If we consider the same character and character state when comparing two placental mammals like humans and cats, however, having three ear ossicles is an ancestral homologue, shared by humans, cats, their most recent common ancestor, and more distant ancestors (Ax 1987, 144). So which characters cladists are interested in—which characters are derived homologues—is relative to the level of comparison (Ax 1987, 144; Sober 1988, 35).



Figure 2-5 A cladogram showing the transition of the number of ear ossicles from the Non-Mammalian Tetrapod condition (one ear ossicle) to the Mammalian condition (three ear ossicles)

⁵ While this is a common example of a derived homologue, new research suggests that 'three middle-ear ossicles' has evolved multiple times within mammals. See Meng et al. 2011 for a review.



Figure 2-6 Ear ossicle transition from the Non-Mammalian Tetrapod condition (A) with one auditory bone (1 = columella auris) and two jaw bones (2 = quadrate, 3 = articular) to the Mammalian condition (B) with three auditory bones (1 = columella auris, 2 = incus, 3 = malleus) revised from Fig. 43 of Ax 1987, 145

At each level, however, there are multiple ways to individuate the characters and their states. The *columella auris*⁶ is the single ear ossicle found in non-mammalian tetrapods as well as mammals (Ax 1987, 145). The shape of this auditory bone in mammals differs greatly from its shape in non-mammalian tetrapods such that the character '*columella auris*' could have two or more character states, each designating a shape (see Figure 2-6). Similarly, two of the jaw bones in non-mammalian tetrapods, the *quadrate* and the *articular*, are the same bones as (homologous with) two of the ear ossicles in mammals, the *incus* and the *malleus* respectively (Ax 1987, 145). So it would be reasonable to individuate the '*quadrate-incus*' character and the '*articular-malleus*' character, each with multiple character states to designate its shape variation. If we maintain the same number of possible states under this character individuation as we had

⁶ In current use, *stapes* is the name for this mammalian ear ossicle.

for the 'one' versus 'three' 'number of ossicles' character, platypus and humans share the '*columella auris*' character of state '1', the '*quadrate-incus*' character of state '1', and the '*articular-malleus*' character of state '1' with their most recent common ancestor. For this individuation of tetrapod ear ossicles, then, there are three derived homologues uniting mammals rather than just one.

Ax (1987, 146) makes it clear that the original individuation, 'one' versus 'three' ear ossicles, is "no longer of any use" if we are comparing types of mammals or species within one of the types of mammals (humans compared to cats) because under such phylogenetic analyses all the organisms have the same character state for the 'number of ear ossicles' character. He does not, however, discuss the possibility of using an individuation like the second articulated above to represent the transition from one to three ear ossicles. So it is not clear whether the transition from one to three ear ossicles in the evolutionarily novel ancestor of mammals should be represented as one evolutionary change or three. It seems, from this example, that there are multiple ways to individuate the same trait into characters and each of these individuations results in a different quantification of evolutionary change. Since phylogenies are inferred by selecting the cladogram which represents the fewest evolutionary changes, this ambiguity in character individuation is troublesome. It so happens that the phylogeny of mammals remains the same under either individuation. But the same is not true for snakes in the following example.

There has been abundant debate in palaeontology journals about the most appropriate character set for description of a primitive snake with hind limbs found in Israel in 1979 (Caldwell and Lee 1997; Lee and Caldwell 1998; Zaher 1998; Caldwell 2000; Zaher and Rieppel 2002). *Pachyrhachis problematicus* (Haas 1979) has many features in common with present day Macrostomatan snakes (large-mouthed snakes like Pythons) and also exhibits well-developed hind limbs (Rieppel et al. 2003, 537). Proposed character sets for this organism have varied substantially. Some emphasize the highly mobile skull and jaw that *Pachyrhachis* has in common with Macrostomatans and some emphasize the relatively well-developed hind limb which differentiates it from all snakes.

When palaeontologists use character sets including only cranial characters the resultant cladogram shows *Pachyrhachis* as a Macrostomatan snake (Tchernov et al. 2000, 2012; Rieppel et al. 2003, 553). Figure 2-7 shows a revision of the cladogram from Tchernov et al. (2000) in which some species have been grouped into their accepted more inclusive clades for ease of comparison with Figures 2-8 and 2-9. When characters behind the head, post-cranial characters, are also included and the hind limb is counted as a single character in the character set of *Pachyrhachis*, the resultant cladogram includes it as the "sister-group to Macrostomatans" within snakes (Zaher 1998, 2; Zaher and Rieppel 2002, 108; Rieppel et al. 2003, 553). Figure 2-8 shows a revision of such a cladogram. If the pelvic girdle and hind limb elements are all counted as separate characters, *Pachyrhachis* is shown to be a transitional form between lizards and snakes⁷ (Caldwell and Lee 1997, 708; Lee and Caldwell 1998, 1544; Caldwell 2000, 188; Rieppel et al.

⁷ This is presented by Rieppel et al. 2003 as requiring inappropriate over-splitting of the hind limb and pelvic girdle, but when the characters in the skull (cranial characters) are individuated differently as well (see Caldwell and Lee 1997; Lee and Caldwell 1998; and Caldwell 2000), the placement of *Pachyrhachis* as basal to all snakes does not require the inclusion of as many hind limb characters.

2003, 553-554). Figure 2-9 shows a revision of a cladogram presented by Lee and Caldwell (1998, 1544).



Figure 2-7 Most parsimonious cladogram for individuation including only cranial characters for *Pachyrhachis;* revised from Fig. 3 in Tchernov et al. (2000, 2012)



Figure 2-8 Most parsimonious cladogram for individuation including cranial characters, post cranial characters, and single hind limb character for *Pachyrhachis;* revised from Fig. 1 in Zaher (1998, 2)



Figure 2-9 Most parsimonious cladogram for individuation including cranial characters, post cranial characters, and multiple hind limb and pelvic girdle characters for *Pachyrhachis;* revised from Fig. 16 in Lee and Caldwell (1998, 1544)

Biologists concerned with the origins of snakes and the phylogenetic placement of *Pachyrhachis* are well aware that the character set used for comparison of *Pachyrhachis* with other organisms determines which cladogram is most parsimonious. They debate at length how many and which parts of the skull and hind limb are appropriate to code as characters (Caldwell and Lee 1997; Lee and Caldwell 1998; Zaher 1998; Caldwell 2000; Zaher and Rieppel 2002; Tchernov et al. 2000; Rieppel et al. 2003; Rieppel and Kearney 2007). If the skull is "split" into a large number of characters while the hind limb is "lumped" into fewer characters, *Pachyrhachis* is most parsimoniously classified as a macrostomatan snake (Rieppel and Kearney 2007, 105). If such a classification were an accurate representation of evolutionary history, this would constitute evidence for a reversal from near complete limb loss in snakes to full hind limb development (Rieppel and Kearney 2007, 105). On the other hand, if the skull is "lumped" into a smaller

number of characters and the hind limb is "split" into more characters, *Pachyrhachis* is most parsimoniously classified as a transitional form between lizards and snakes (Rieppel and Kearney 2007, 105). Since it is up to each biologist to determine the most appropriate character individuation for her investigation, each such individuation may contain a different character set for *Pachyrhachis*, and each character individuation may result in a different most parsimonious classification, there does not appear to be only one most parsimonious classification for *Pachyrhachis* (Richards 2003; Rieppel and Kearney 2007, 105).

2.5 The Character Individuation Problem: An Introduction

As discussed in section 2.2, cladists use phylogenetic inference (and other taxonomic schools use their preferred methods) in order to reconstruct evolutionary history. Since evolutionary history is just that, history, it is assumed that it actually occurred via some set of events and that a reconstruction of that history will involve mapping the order of those events. Assuming that time is linear, this view of evolutionary history implies that only one reconstruction can be historically accurate. In the *Pachyrhachis* example, then, only one classification can be a historically accurate mapping of evolutionary history.

Selection of a correct reconstruction by cladists is based on the use of parsimony. This assumption that evolutionary change is improbable allows cladists to pick out the reconstruction which involves the least number of changes as being the best phylogenetic inference. Evolutionary change is quantified by comparing homologues and designating differences between homologues as different states of the same character. So cladists can quantify change in the number of vertebrae by assigning 'less than 100' as the state of the 'vertebrae number' character for one organism while assigning 'between 100 and 300' as the state of the same character in a different organism. Designation of these differences and individuation of the homologues into characters can be done in multiple ways, resulting in multiple character sets. The hind limb of *Pachyrhachis* (a homologue of the hind limb of lizards and the vestigial hind limb in Pythons) can be individuated as a single character with some number of possible states or it could be parsed into more characters, each with their own designated states. So quantification of evolutionary change (individuation of characters) can be done in multiple ways and the selection of the best phylogenetic inference is dependent on these individuations. In this way, multiple character sets can lead to multiple 'most parsimonious' or 'correct' evolutionary reconstructions.

This problem becomes philosophically pressing if cladists do not have an objective way to choose a character individuation for application of parsimony. In the next chapters I will discuss the treatment of this problem by two philosophers, Richard Richards (2003) and Rasmus Winther (2009). Richards (2003) suggests that the individuation of characters by cladists is arbitrary. If this is the case, the inferences that cladists make using parsimony lose the objectivity that made Cladism so popular in the first place (Richards 2003). Arbitrary character individuation would undermine the use of parsimony for phylogenetic inference and result in failure on the part of cladists to objectively map out evolutionary history. Winther (2009), on the other hand, suggests
that abstraction⁸ of characters is merely theory laden and the problem is actually reification of characters that are not the 'real' characters of the organisms under study. He unites character abstraction criteria proposed by biologists and philosophers as a possible set of criteria for distinguishing real characters from reified ones (Winther 2009).

In Chapter Three I discuss Richards' (2003) approach to the character individuation problem, how he arrives at his pessimistic conclusions, and why such pessimism is unwarranted. I discuss Winther's (2009) more optimistic approach in Chapter Four, explaining how his proposed criteria for character abstraction seem to solve the character individuation problem, and why character individuation remains a problem. I conclude in Chapter Five with a review of the character individuation problem, a discussion of the insights gained from the approaches taken by Richards (2003) and Winther (2009), and summarize some points for philosophers to keep in mind when dealing with this problem.

⁸ Winther (2009) focuses on abstraction of characters rather than individuation of them. I distinguish between the two in depth during my discussion of his view but in brief, 'abstraction' is the recognition of shared traits while 'individuation' is parsing them into characters and states.

Chapter Three: Richards' View of the Problem

In this chapter I discuss a pessimistic approach to the character individuation problem and how such a view fails to establish conclusively that there is a problem. This approach to the character individuation problem is from Richards' (2003) "Character Individuation in Phylogenetic Inference," the first philosophical work devoted entirely to analysis of the character individuation problem. After outlining Richards' (2003) approach and associated arguments, I discuss the reasoning provided for each aspect of the argument. Two primary problems with this argument arise; I discuss them each independently as well as how they undermine Richards' (2003) attempt to establish that the character individuation problem is actually a pressing problem.

3.1 Overview of Richards' (2003) Approach

Richards' (2003) approach to the character individuation problem focuses on a three-fold separation in cladistic method: the individuation of characters, the formation of a data set, and the application of parsimony to the resultant set of characters. For Richards (2003, 265), the source of objectivity in the cladistic method is the use of the parsimony principle, "usually...understood to be an unequivocal method of hypothesis evaluation." His reasons for this claim are discussed below in section 3.1.2. In order to argue that cladistic use of parsimony is not as decisive as it seems, Richards (2003) first explains that "it is possible to individuate characters in different ways, with different parsimony implications." While most of the previous chapter was devoted to explaining and illustrating this fact, section 3.1.3 below reviews Richards' (2003) discussion of it.

Next, Richards (2003, 277) argues that cladists lack a "single unambiguous character individuation criterion," the explication of this argument is in section 3.1.4 below. Finally, Richards (2003) argues that any objectivity acquired by use of parsimony evaluation in cladistics is undermined by multiple outcomes.⁹ Section 3.1.5 outlines Richards' (2003) reasons for this claim.

Once Richards (2003, 265) has argued that parsimony as it is used by cladists is not the "unequivocal method of hypothesis evaluation" that it appears to be, he discusses the implications of his conclusion and how he thinks it must be dealt with. If the use of parsimony in phylogenetic inference is equivocal, then phylogenetic inference itself "may well be subjective or arbitrary." (Richards 2003, 265) Sections 3.1.6 and 3.1.7 below discuss Richards' (2003) reasons and reaction (respectively) to this conclusion. He suggests that the key to solving the character individuation problem is to rethink and redefine characters entirely.

3.1.1 'Objective' and 'Subjective' in Richards (2003)

Before delving into Richards' (2003) approach to the character individuation problem, it is important to understand what Richards means by 'objective' and 'subjective.' While the use of 'objective' is often ambiguous in philosophy of science, the two most common usages are 'objective' as unbiased or impartial, and 'objective' as taken from mind-independent existence or truth. (Godfrey-Smith 2003, 6) After

⁹ Richards (2003) only uses 'objective' and 'objectivity' in quotation marks to emphasize that it is cladists who believe their methods to be objective as a result of parsimony. In his own arguments he prefers to use 'subjective,' but his arguments are nevertheless about objectivity. I explain the sense in which he is concerned with objectivity in section 3.1.1.

discussing the impartiality of mathematics in comparison to the impartiality of the cladists' parsimony principle, Richards states that "given a set of characters, the cladistic method might be unequivocal, hence "objective" in the manner suggested, but the outcome of the method depends on the formulation of the data set." (Richards 2003, 268) While he is not explicit about what he means by "objective" here, the "manner suggested" by Richards' previous section is that of an unbiased or impartial objectivity.

This objectivity as absence of bias is contrasted with subjectivity. Godfrey-Smith (2003, 12) describes this use as referring to a "distinction, perhaps a vague one, between good and bad influences on belief." Such a distinction "makes some sort of contrast between two ways of forming beliefs, one way that is dependent on caprice, prejudice, or point of view, and one that avoids such "subjective" influences." (Godfrey-Smith 2003, 12) Distanted and the this time of distinction.

12) Richards' use of 'objective' and 'subjective' seem to make this type of distinction.

One advantage claimed by cladists over competing methods was that their method was "objective" because it forced the acceptance of the most parsimonious phylogenetic hypothesis, and the rejection of all other hypotheses, regardless of our preferences or desire. (Richards 2003, 274)

'Objective,' for both Richards (2003) and the cladists he critiques, seems to mean unbiased while 'subjective' means biased. Richards (2003) connects this distinction to one between 'unequivocal' and 'subjective'. In this distinction, subjective still means biased—based on "preference or desire." (Richards 2003, 268) "Unequivocal," for Richards means not only unambiguous but also immune to subjective influence.

> One advantage of this approach is that it *seems* to be unequivocal. Like simple addition, cladistic parsimony unambiguously specifies the outcome at each step. No

preference or desire can change the fact that 2 + 3 = 5, and 5 is less than 6. (Richards 2003, 268)

This connection of 'unequivocal' to 'objective' as meaning a non-subjective way to form beliefs—specifically beliefs about which hypothesis should be preferred—is how Richards comes to conclude that only unequivocal methods can be objective methods.

> The idea of this objectivity argument is that the application of the parsimony principle to the data provides a rule that forces the acceptance or rejection of hypotheses, just as simple addition forces us to a certain conclusion. No preference or desire can therefore play a part in hypothesis evaluation. No one can, it is presumed, save a preferred phylogenetic hypothesis by weighing more heavily the characters that favour that hypothesis. (Richards 2003, 275)

While Richards (2003) connects 'unequivocal' and 'objective' in this way, he does not do so explicitly, but by continued use of the assumption that any factors contributing to variation in phylogenetic outcomes are subjective influences. He assumes that the only non-subjective decision procedure is one which unequivocally leads every researcher who applies it to the same decision. I argue against this assumption in section 3.2.1 and discuss this further in section 4.2 when I contrast Winther's (2009) use of 'subjective' and 'objective' with Richards' (2003).

3.1.2 Parsimony as an Unequivocal Method

When Richards (2003) provides a short lesson on the methods of process cladists, he emphasizes the use of characters and the parsimony principle to produce taxonomic classifications. Since this method utilizes the parsimony principle at several stages—the initial formation of cladograms, rooting those cladograms, and the resolution of conflicts produced by non-homologous character data—Richards (2003) suggests that parsimony

is meant to be the source of objectivity in phylogenetic inference.

Like simple addition, cladistic parsimony unambiguously specifies the outcome at each step. No preference or desire can change the fact that 2 + 3 = 5, and 5 is less than 6. And no preference or desire can change the fact that the phylogenetic hypothesis (AB)C above requires 8 changes, while the hypothesis (BC)A requires twelve changes, and since eight is less than twelve, (AB)C is therefore more parsimonious than (BC)A. Since (AB)C is the most parsimonious hypothesis of the three, the other hypotheses must be rejected. (Richards 2003, 268)

He seems to adopt this view from the cladists whose methods he discusses. Wiley (1981, 20) describes the most parsimonious hypothesis as the one "with the fewest ad hoc statements"; Eldredge and Cracraft (1980, 67) state that parsimony "specifies the most preferred hypothesis;" and Ax (1987, 221) compares hypotheses by suggesting that "the principle of parsimony requires" one in particular. Richards (2003, 275) explains that the point of using parsimony is to prevent "preference or desire" from playing an active role in hypothesis evaluation. "No one can, it is presumed, save a preferred phylogenetic hypothesis by weighting more heavily the characters that favour that hypothesis." (Richards 2003, 275) The use of parsimony makes cladists take the data seriously because it is meant to be unequivocal (Richards 2003, 275).

3.1.3 Different Character Sets can have Different Parsimony Implications

After explaining how the use of parsimony for phylogenetic inference "*seems* to be unequivocal" Richards (2003, 268) suggests that we must doubt its objectivity because there are multiple ways to individuate characters. "Given a set of characters, the cladistic

method might be unequivocal, hence "objective," in the manner suggested, but the outcome of the method depends on the formulation of the data set." (Richards 2003, 268-269) He establishes by example that no matter what type of characters—morphological, molecular, genetic, or behavioural—are included in the data set there is ambiguity in how they are individuated.



Figure 3-1 Richards' (2003) hypothetical phylogenetic inference of taxa A, B, and C including the three ear ossicles of mammals individuated as a single character (cladogram a and cladogram b) or three separate characters (cladogram c and cladogram d) where x and y are characters assumed by Richards to be the same in either case

Richards (2003) begins by discussing Ax's (1987) Mammalian ear ossicle example with reference to a hypothetical set of taxa, A, B, and C. Stipulating that "the phylogenetic hypothesis (AB)C" is most parsimonious when Ax's (1987) 'three ear ossicles' are individuated as a single character (Figure 3-1a), Richards points out that three ear ossicles could represent multiple evolutionary changes if each ossicle is individuated as its own character (Richards 2003, 269). In Richards' hypothetical classification example the single 'three ear ossicles' character is shared by A and C but not by B. So if each ossicle were a separate character the hypothesis (AC)B (Figure 3-1d) would be favoured by two extra characters while (AB)C (Figure 3-1c) would represent two extra evolutionary changes. In this case, Richards (2003, 270) explains, "(AC)B would be the most parsimonious hypothesis."

Ax (1987, 107) discusses the spines of anteaters as an example of features which cannot be recognized as "separable" elements, "that can only be done for the coat of spines in its totality." Richards (2003, 270) points out that "if we regard each spine as a character, then given the number of spines possessed by each, we may be forced to infer that the anteater and porcupine are closely related." He claims that Ax does not explain his reasons for rejecting this possibility and that without a clear "principle" stipulating what "can be considered a separable element," character individuation is ambiguous (Richards 2003, 270).

Richards (2003, 270) goes on to establish that this same "ambiguity" occurs for characters other than morphological ones like spines and ear ossicles. Behavioural characters like 'displaying' in wood storks could be individuated as 'gaping,' 'balancing,' and 'preening,' the three components of the behaviour described by Eldredge and Cracraft (1980, 46; Richards 2003, 270-271). Similarly, we could individuate molecular characters in terms of their "nucleotides, nucleotide sequences, proteins or genes" (Richards 2003, 271). He suggests that for DNA we could "individuate each change in a nucleotide" or "sequence that codes for a particular protein" as characters but that these two data sets would be "inconsistent" (Richards 2003, 271). Within each character type "different character individuation schemes can be expected to produce conflicting outcomes—favouring different phylogenetic hypotheses and the taxonomies that result from them." (Richards 2003, 271)

3.1.4 Lack of an Unequivocal Character Individuation Criterion

Richards (2003, 271) suggests that "multiple ways to identify and individuate characters is certainly a problem for parsimony-based approaches to phylogenetic inference, since hypothesis evaluation depends on which individuation scheme is chosen." If the problem is as Richards states, then arbitrary or subjective individuation of characters or "choice of individuation schemes" would result in arbitrary or subjective hypothesis evaluation (Richards 2003, 271). He suggests that this could be avoided if there were "an unequivocal principle of character individuation." (Richards 2003, 271)

Beginning with Ax (1987), Richards (2003) systematically rejects four possible "principles" based on the fact that multiple ways of individuating characters are possible under each. Ax (1987, 105) uses "separable element" in his definition of the word "feature" (which he prefers to "character") as well as his discussion of how to individuate the spines of the spiny anteater (Ax 1987, 107). While Ax does not define "separable element," he dictates that "a feature of an organism which can be distinguished from other corresponding units, or perhaps better, elements, of one and the same organism" are valid features (Ax 1987, 105; Richards 2003, 271). Richards (2003) points out that under this definition, both 'three ear ossicles' and 'columella auris' are valid features even though one is a part of the other. Similarly, every individual spine on the spiny anteater, the section of "tail spines," the section of "back spines," and the spiny coat as a whole are all valid features under this definition (Richards 2003, 271-272). While Ax (1987, 107) stipulates that of all these possible spine features, only "the coat of spines in its totality" is a "separable element," he does not provide Richards with the "principle he is using to reject the possibility that each spine can be considered a separable element." (Richards 2003, 270). Under the 'separable element' principle, Richards (2003, 271-272) finds that there are multiple ways to individuate characters, some of which are rejected by the proponent of that principle, so Richards rejects this type of "separability" as a potential "unambiguous character individuation criterion."

Richards (2003, 272) also rejects the notion that characters could be "separable because they have distinct functions." He points out that cladists Grande and Rieppel (1994, 246) recognize the ambiguity of a functional character individuation criterion and returns to the ear ossicle example to illustrate:

> We could therefore individuate three ear ossicles as a single character by virtue of its functioning as a whole, or we could individuate each ossicle for its function within this whole. Likewise, the various characteristics of each ossicle could be individuated according to their functions. (Richards 2003, 272)

So 'functionally separable' as an individuation principle would allow characters to be individuated in a variety of ways, as functional complexes, functional units within complexes, or particular functional characteristics of functional units. Since this principle, like the first one, allows for multiple ways of individuating characters, Richards rejects it, calling it ambiguous as well (Richards 2003, 272). His rejection of individuation based on developmental independence is on the grounds that "it is equivocal in just the way the other criteria are." (Richards 2003, 272) Since developmental pathways interact to form organisms, Richards (2003, 272) suggests that it might be possible to "identify a developmental pathway for each ear ossicle as well as for the complex of ossicles itself." He also emphasizes the complexity of development as a secondary reason for being dissatisfied with such criteria. Even if we could trace a single developmental pathway back to a single gene, "genes themselves interact in complex ways" such that we are brought back to the same problem again; it is unclear where to divide the complexes of genes and developmental pathways in order to individuate them into characters (Richards 2003, 272-273).

The final type of individuation criterion Richards (2003) considers and rejects is one based on how similarities are recognised, named, and communicated. Richards considers Wiley's (1981) communication criterion and Eldredge and Cracraft's (1980) perception criterion to both be principles based on this sort of practical recognition of characters. Wiley (1981, 8) suggests that characters be identified in a practical way—by what is done with them rather than by something about them. He suggests identifying them based on description, and that effective communication of a feature would result in it being considered "real" (Wiley 1981, 116). For Wiley (1981, 8), characters are parts of organisms which "may be described, figured, measured, weighed, counted, scored, or otherwise communicated by one biologist to other biologists." Richards considers this criterion to be the same as Eldredge and Cracraft's (1980) perception criterion for characters. Eldredge and Cracraft (1980, 30) suggest that characters are the names of similarities, that perception of similarity is how biologists determine what is "comparable." Like Wiley (1981), Eldredge and Cracraft (1980) are taking a practical approach to individuating characters based on recognition and communication. Richards rejects them both on the same grounds:

The ear ossicles in two species may be correctly perceived as similar in proportion, shape, or in any other way, but that fact does not tell us whether there are three similarities or one, any more than it tells us whether there are three characters or one. (Richards 2003, 273-274)

We can describe, figure, measure, and do any number of practical things to three ear ossicles as a complex or to each ossicle individually. We can also perceive, name, and communicate about three individual ear ossicles or an ear ossicle complex. Just as he did with the other three potential 'principles of character individuation', Richards (2003) determines that recognition and communication principles allow for multiple ways to individuate characters and thus are ambiguous.

3.1.5 Parsimony Evaluations with Multiple Outcomes

Richards (2003, 275) is particularly concerned with the ambiguity in character individuation criteria because given a single set of characters, parsimony stipulates which one phylogenetic hypothesis must be accepted. In the event that multiple sets of characters are accepted, there would seem to be multiple 'most parsimonious' hypotheses. But having more than one 'most parsimonious' hypothesis seems counterintuitive such that one would have to be selected as more parsimonious than the other. If selection of one data set over the other cannot be made objectively then parsimony seems ill equipped to select one hypothesis over the other in an objective way. Richards (2003, 275) is concerned that "if there is no satisfactory way to tell how many changes a phylogenetic hypothesis presupposes, there is no satisfactory way to determine how parsimonious that hypothesis is."

A second concern which Richards (2003) raises is about the formation of the data set. Recall that Richards (2003) considers 'application of a character individuation criterion' and 'formation of the data set' to be separate aspects of phylogenetic inference. "Even if there were an unequivocal principle of character individuation, decisions must still be made about which characters to include in the data set." (Richards 2003, 275) Here, Richards is concerned about the wide variety of character types from molecular to behavioural. He points out that different specialists tend to use different types of characters in their data sets.

> Molecular phylogeneticists, are, unsurprisingly, more likely to include molecular characters. Traditional morphologists are more likely to use morphological characters. And within this group, there is variation. Vertebrate morphologists typically rely on muscles and skeletal structure for their characters, while invertebrate morphologists are more likely to focus on genitalia. More recent trends have been toward characters based on neuroanatomical patterns and sperm morphologies (Wake 1994, 174). The specific behavioural characters to include in a data set will similarly vary among phylogeneticists. (Richards 2003, 276)

While Richards does not explain why he thinks these various types of character sets would constitute multiple outcomes for the same parsimony evaluation, he does discuss problems with using multiple types of characters within the same set. He expresses concerns that parsimony would have to weigh a nucleotide as equal to a morphological complex like 'three ear ossicles' but "not all characters seem equivalent." (Richards 2003, 276) Redundancy introduced by using both a morphological character and the genes or developmental pathways involved in the production of that morphological character in a single character set is another concern. "If we count both, we seem to be counting the same character twice." (Richards 2003, 276)

Richards (2003) also brings up a way in which multiple outcomes can result from the use of parsimony even if only one (evenly weighted and non-redundant) set of characters is used. Different parsimony algorithms are used by cladists to determine overall parsimony, "each of which typically picks out different phylogenetic hypotheses as the most parsimonious" (Richards 2003, 276). With no single way to establish relative degrees of parsimony, the objectivity that is supposed to result from the use of parsimony is undermined.

> So which hypothesis is most parsimonious depends not only on character individuation schemes, and choice of characters for the data set, but also on which parsimony algorithm is used. (Richards 2003, 276)

Just as phylogeneticists could "identify and individuate similarities in such a way as to license the phylogenetic inference they desire or prefer," they may choose a character type or parsimony algorithm which will result in a particular desired outcome (Richards 2003, 275).

3.1.6 Subjectivity in Phylogenetic Inference

Richards (2003, 275) emphasizes that "the application of the parsimony principle to the data provides a rule that forces the acceptance or rejection of hypotheses, just as simple addition forces us to a certain conclusion." But if the character data is individuated subjectively, the hypothesis parsimony selects will be equally subjective. Similarly, if the characters are arbitrarily individuated, the most parsimonious hypothesis is arbitrary as well. That "2 + 3 = 5" means something, whether the numbers were drawn out of a hat or count the number of goals scored in a hockey game, is a special characteristic of mathematical equations. For taxonomists, however, if the number of evolutionary changes represented by a cladogram may as well be drawn out of a hat, the statement "most parsimonious" seems meaningless. "One advantage claimed by cladists over competing methods was that their method was "objective" because it forced the acceptance of the most parsimonious phylogenetic hypothesis." (Richards 2003, 274). But if Richards (2003, 274) is right about the subjective individuation of characters for application of parsimony "forcing" the acceptance of the 'most parsimonious' hypothesis, then the cladistic method is not objective.

Richards (2003, 275) thinks that without an unequivocal principle for determining the data set for the application of parsimony, that the agendas of taxonomists could determine which hypothesis is accepted.

> There is no accepted principle of character individuation that can unambiguously determine the data set—the set of characters that factor in parsimony considerations. Phylogeneticists might well identify and individuate similarities in such a way as to license the phylogenetic inference they desire or prefer. If so, it is unclear how the application of parsimony can provide a satisfactory basis for phylogenetic inference. (Richards 2003, 275)

If parsimony is the basis of Phylogenetic Inference and, more importantly, the source of objectivity for phylogenetic inference, its failure results in the failure of phylogenetic inference to be objective. Since phylogenetic inference is employed by the dominant school of taxonomy, process cladistics, if Richards (2003, 277) is right, "a lot of resources are being misspent on a misguided approach to phylogenetic research."

3.1.7 Rethinking the Character Concept

Richards (2003) notes, as I do in the previous chapter, that while the character individuation problem is a problem for cladists, it is also a problem for evolutionary taxonomists and pheneticists. Both of these schools of taxonomy depend on characters and, as Richards (2003, 277) discusses, "seem to be employing an ambiguous character criterion as well." The problem that all of these taxonomists have, according to Richards (2003), is that they do not have an adequate character concept on which to base an unambiguous character individuation criterion. His solution is thus to rethink the character concept entirely.

"This problem in character individuation is a philosophical problem in that it demands that we think about an ontological category—what counts as a character." (Richards 2003, 277) Winther (2009) works on this project by setting out a group of criteria to pick out "real" characters. I will discuss this type of solution further in the next chapter when I introduce Winther's (2009) proposed view of the character problem. Richards (2003) suggests one guideline for the pursuit of a solution to the character individuation problem:

> The goal of phylogenetic inference is the reconstruction of the branching order of the evolutionary past. A satisfactory character individuation scheme—and character concept must surely function to support that goal. What that involves is a project worthy of pursuit. (Richards 2003, 278)

Richards (2003) does not offer any further discussion about what such a character concept might look like nor what would make the corresponding character individuation scheme satisfactory.

3.2 Objections to Richards' (2003) Approach

I disagree with Richards' (2003) approach to the character individuation problem on two points. First, his argument that cladists lack an 'unequivocal principle of character individuation' conflates the individuation procedure with its possible outcomes. Section 3.2.1 disambiguates '*unequivocal principle of character individuation*' from '*principle of unequivocal character individuation*' and argues that Richards' (2003) conclusion is premature. Second, his argument that we should doubt the objectivity of the use of parsimony in phylogenetic inference misconstrues parsimony evaluation and unrealistically demands information about relative parsimony—how parsimonious one specific hypothesis is as compared to another specific hypothesis. Section 3.2.2 clarifies how phylogenetic parsimony evaluations differ, how such differences affect claims about relative parsimony, and explains that Richards' (2003) argument does not lead to scepticism about cladistic parsimony.

3.2.1 Against 'Lack of an Unequivocal Character Individuation Criterion'

After Richards (2003, 271) explains how different character sets can lead to different parsimony implications and that this would be a serious problem for cladists if "choice of individuation schemes were itself arbitrary or subjective," he suggests a way to avoid this problem. An "unequivocal principle of character individuation" would ensure that character individuation is not arbitrary or subjective (Richards 2003, 271). So what is an *'unequivocal principle of character individuation'*? Richards (2003) does not provide a positive account of what would count as an *'unequivocal principle of character individuation'* but there seem to be two possible meanings.

Richards (2003, 268) may want an 'unequivocal principle' like the principle of parsimony which he argues "unambiguously specifies the outcome at each step" as simple addition unambiguously specifies the sum of two numerical inputs. So an 'unequivocal principle' for Richards (2003) is one which consistently provides a single outcome for a specified input. An 'unequivocal principle of character individuation' would, then, unambiguously specify a single outcome for each input.

On the other hand, we could take Richards' (2003, 271) to want the opposite of what he rejects. He rejects 'principles' which allow more than one character individuation. Ax's (1987, 105) "separable element" allowed multiple character sets to be individuated from a single feature, 'three ear ossicles': the set including the character complex 'three ear ossicles' and the set including three individual characters, one for each ossicle. Richards rejected this and the other three potential 'principles' for the same reason, they allowed for multiple individuations of the same feature. Perhaps, then, Richards' (2003, 271) "unequivocal principle of character individuation" is a principle which specifies the same individuation for a given feature under any circumstance.

Richards' (2003, 278) only positive conclusion states that a satisfactory principle of character individuation must function to support the goal of phylogenetic inference— "the reconstruction of the branching order of the evolutionary past." So in order to determine what Richards (2003) wants let us consider which type of principle would support that goal. Does a principle which unambiguously specifies a single outcome for each taxonomic input, an *unequivocal principle of character individuation*, support the goal? Or does a principle which specifies the same individuation for a given feature under any circumstance, a *principle of unequivocal character individuation*, support it?

Given the fact that 'reconstructing the branching order of the evolutionary past' is mapping out steps in evolution, a principle of unequivocal character individuation seems to be opposed to the goal of phylogenetic inference. Ax's (1987, 146) discussion of the lack of use of a single 'three ear ossicles' character for comparison of species of mammals makes this clear. Recall from the first example in section 2.4 that the individuation 'three ear ossicles' versus 'one ear ossicle' distinguishes mammals as a group from all other tetrapods. Platypus, human, and their most recent common ancestor have the same three auditory bones so the character 'three ear ossicles' is a derived homology of mammals (Ax 1987, 146). However, in the comparison of two placental mammals (human with cat for example), 'three ear ossicles' is an ancestral homology and so has no bearing on phylogenetic evaluations within placental mammals (Ax 1987, 146). It may be the case that each auditory bone has evolved in different ways such that the complex differs among placental mammals but the number of ear ossicles remains the same. In such a case it would seem that individuating the ossicles in a different way would be the only way to account for the change. Similarly, it would not make sense to individuate the three auditory bones separately in cases when none of the organisms under comparison have auditory bones. Depending on the organisms included in the analysis, a different individuation of characters is required in order to 'reconstruct the branching order of the evolutionary past'.

One of Richards' (2003) own examples emphasizes this point as well. He discusses the fact that different specialists tend to individuate characters of the type that they specialize in. "Vertebrate morphologists typically rely on muscles and skeletal structure for their characters, while invertebrate morphologists are more likely to focus on genitalia." (Richards 2003, 276) What Richards (2003) does not seem to take away from this example is that vertebrates evolve in different ways from invertebrates; vertebrates tend to vary in musculature and skeletal structure while invertebrates do not have the same type of skeleton or muscles. Invertebrate genitalia vary much more than vertebrate genitalia such that those are the characters available for classifying them. A principle which specifies the same individuation for a given feature under any circumstance could not account for the difference in variability among different features of different organisms. Taking such differences into account as well as the evolution of species, organisms, and their parts, a '*principle of unequivocal character individuation*' cannot support the goal of phylogenetic inference.

Richards (2003) should want an '*unequivocal principle of character individuation*' as he claims to, then. A principle which unambiguously specifies a single outcome for each taxonomic input could account for differences in variability as well as the evolution of species, organisms, and their parts. Our 'three ear ossicles' character, for example, could be part of the character set for cats when they are compared to nonmammalian tetrapods like lizards and snakes but would not be part of the character set of cats if we compared them to dogs. Similarly, if we compare a vertebrate like cats to an invertebrate like lobster, genitalia characters would not be included in either character set. But if we compared only invertebrate species there may be multiple genitalia characters in the character sets of each species. In this way, application of an '*unequivocal principle* of character individuation' would output a different character individuation to correspond with different taxonomic comparisons.

If an '*unequivocal principle of character individuation*' like the one described above is what Richards (2003) wants, however, he has not established that cladists lack one. His rejection of each of the potential 'principles' of character individuation was based on the fact that the principle allowed multiple character individuations for the same feature. But in order to specify a different character individuation for each taxonomic comparison, a principle of character individuation must allow for multiple character individuations for the same feature. So Richards' (2003, 275) conclusion that "there is no accepted principle of character individuation that can unambiguously determine the data set" is premature.

3.2.2 Against 'Parsimony Evaluations with Multiple Outcomes'

Richards (2003) suggests that variation in character individuation should lead us to be sceptical about the unequivocal nature of parsimony application. He thinks that multiple parsimony outcomes from multiple character sets detract from the claim that a certain phylogenetic hypothesis is the most parsimonious hypothesis.

> At best, we should doubt that our judgments about the relative parsimony of hypotheses are well grounded. At worst, we might doubt that there are any facts about the relative parsimoniousness of particular phylogenetic hypotheses. If so, parsimony judgements would then be arbitrary or subjective. In either case, we cannot establish relative degrees of parsimony. (Richards 2003, 275)

These conclusions seem premature, however, because there are problems with his notions of relative parsimony and multiple parsimony outcomes. Richards (2003) fails to recognise that multiple outcomes are only a problem for parsimony if a single parsimony evaluation can result in more than one outcome. When it is made clear what a phylogenetic parsimony evaluation entails, it becomes clear that Richards (2003) has not established a problem for parsimony as it is used in phylogenetic inference. Similarly, Richards' (2003) problem with the inability to establish relative parsimony seems to assume that if w is more parsimonious than x, and y is more parsimonious than z, then we should be able to conclude something about the relative parsimony of x and y. That we cannot make such a conclusion, however, does not necessarily mean there is something wrong with our original parsimony claims or parsimony principle itself; x and y may not be comparable hypotheses.

In order to illustrate how confusion about relative parsimony may occur, let us return to Richards' (2003, 268) comparison of the parsimony principle to addition. He says that "like simple addition, cladistic parsimony unambiguously specifies the outcome at each step. No preference or desire can change the fact that 2 + 3 = 5, and 5 is less than 6" (Richards 2003, 268) Richards' (2003, 275) suggestion to doubt parsimony results from his concern that variation in the characters to which parsimony is applied results from differences in preference or desire. He does not seem to consider the possibility that variation in character individuation could result from facts about the evolutionary process and organisms under study. If we were to ignore such factors, we could find reason to doubt the objectivity of addition as well.

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The principle of addition can tell us that 4 + 5 = 9. The addition of 4 metric tonnes¹⁰ to 5 metric tonnes gives us a total of 9 metric tonnes. Similarly, the addition of 4 bushels¹¹ to 5 bushels gives us a total of 9 bushels. If we attempt to perform addition on these two sums, however, we run into a problem. The addition of 9 and 9 is 18 but the addition of 9 metric tonnes and 9 bushels is neither 18 metric tonnes nor 18 bushels. This addition cannot be performed without conversion of metric tonnes into bushels or vice versa. Moreover, the conversion happens to be different depending on what is being measured. A bushel of barley has a different weight in metric tonnes than does a bushel of wheat or canola, and a bushel of dried grain has a different weight than does freshly harvested grain. Taking all these factors into account, we could add 9 metric tonnes to 9 bushels of grain but without taking them into account this addition gives a meaningless result. This does not actually give us reason to doubt that there are facts about addition, relative weights, or relative volumes of grain. So why would we doubt parsimony for such reasons?

If we know that w is more parsimonious than x, then we have information about the relative parsimony of w and x; if we know that y is more parsimonious than z, then we have information about the relative parsimony of y and z; these statements, however, do not provide any information about the relative parsimony of x and y. This may be because the comparison of w with x involved a different individuation of characters from the comparison of y and z. The difference might have been as simple as how many characters 'three ear ossicles' constitutes, or the number of states each character had. It

¹⁰ Measure of weight used for the sale of grain.

could also have been the case that there were no common characters between the w-x comparison and the y-z comparison. The w-x comparison may have included only vertebrate species while the y-z comparison may have included only invertebrate species. In all of these cases, the difference in characters results in a difference in parsimony evaluations such that one hypothesis from each (x and y for example) cannot be compared without a whole new parsimony evaluation at best and may not be comparable at all.

Different outcomes may also result if the character set to which parsimony is applied is kept consistent while the parsimony algorithm is changed. "There are multiple algorithms for determining overall parsimony...each of which typically picks out different phylogenetic hypotheses as the most parsimonious." (Richards 2003, 276) Our *w-x* comparison and *y-z* comparison would not provide us any information about an *x-y* comparison in this type of case either. Even if all the characters were the same for all our parsimony evaluations, when the algorithm is changed so too do their outcomes and comparability. Only applications of parsimony to the same character input using the same algorithm can be considered the same parsimony evaluation.

If two possible hypotheses are not included within the same parsimony evaluation, they are not comparable. Attempting to establish relative parsimony for them would be like trying to add 4 bushels to 5 metric tonnes without doing a conversion of units first. So statements about relative parsimony only make sense if they are about hypotheses from the same parsimony evaluation. Since parsimony evaluations differ by the characters involved and algorithms used, the 'same parsimony evaluation' cannot

¹¹ Measure of volume used for the pricing and sale of grain

change its outcome as a result of a different character set or algorithm. If the characters change, it is a different parsimony evaluation; if the algorithm differs, it is a different parsimony evaluation. The different outcomes that Richards (2003) discusses, then, are evidence of different parsimony evaluations rather than evidence that parsimony evaluations have multiple outcomes.

With unrealistic expectations on what phylogenetic parsimony can tell us about the relative parsimony of hypotheses, and ambiguity about what constitutes a unique parsimony evaluation, Richards (2003) comes to a sceptical conclusion about the use of parsimony in phylogenetic inference. Once the scope of each parsimony evaluation and the possible information attainable from it are made clear, however, such scepticism seems to be unjustified. The conclusion that "we cannot determine the relative parsimoniousness of phylogenetic hypotheses, or that there are no facts about the relative parsimoniousness of phylogenetic hypotheses" is premature just as the pessimistic conclusion about character individuation was (Richards 2003, 277).

3.3 Rejection of Richards' Conclusions

Richards' (2003) view of the character individuation problem divides phylogenetic inference into the individuation of characters and the application of parsimony to those characters. Using this dichotomy he argues that "phylogenetic inference, as it is typically practiced, may well be subjective or arbitrary." (Richards 2003, 265) He argues that parsimony is the source of objectivity for phylogenetic inference, and that it fails to provide this objectivity such that phylogenetic inference fails to be objective. His premise that parsimony fails to provide objectivity to phylogenetic

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inference is argued in two ways; first he argues that character individuation is subjective or arbitrary such that parsimony outcomes are also subjective or arbitrary; second, he argues that since parsimony evaluations can have multiple outcomes, the selection of a most parsimonious hypothesis ends up being a subjective selection from a pool of 'most parsimonious' hypotheses.

Section 3.2 discussed the problems with these arguments for the subjectivity of phylogenetic parsimony. The first fails because Richards (2003) does not establish that character individuation is subjective. No matter what he means by an unequivocal principle of character individuation, he has not established that cladists lack one. The second fails because parsimony evaluations do not have multiple outcomes. Multiple outcomes in parsimony are evidence that there are multiple parsimony evaluations being conflated. Without these, Richards (2003) cannot validly conclude that the practice of parsimony in phylogenetic inference is subjective. Since Richards (2003) fails to establish that parsimony as it is used in phylogenetic inference lacks objectivity, he fails

While Richards (2003) fails to demonstrate that phylogenetic inference lacks objectivity such that cladists need to entirely re-evaluate their character concept, he is right to question the individuation of characters by cladists. Richards (2003) makes it evident that individuation of characters by cladists lacks an explicit method or set of criteria. The way Richards (2003) views the character individuation problem, however, does not seem conducive to a solution. While he suggests that a satisfactory character concept and corresponding individuation scheme must support the goal of phylogenetic inference—"the reconstruction on the branching order of the evolutionary past"— Richards (2003, 278) goes no further. He does not suggest any solution or recommend any path of study upon which a solution could be found. In the next chapter, we turn to Winther (2009), who takes a more optimistic approach and offers a potential solution in response to Richards' (2003) pessimism.

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Chapter Four: Winther's Search for Objectivity

In this chapter I discuss an optimistic approach to cladistic character analysis and its attempted response to Richards' (2003) pessimism. It is from Winther's (2009) "Character Analysis in Cladistics: Abstraction, Reification, and the Search for Objectivity." This approach focuses on a distinction between the 'real' characters of evolutionary history—homologues—and those reified because of their superficial similarity to homologues—homoplasies. Winther (2009) suggests that cladistic inference is done correctly when objectivity criteria are applied during character abstraction to ensure that homologues are exclusively used as taxonomic data.

4.1 Overview of Winther's (2009) Approach

Winther (2009) holds that the only parts, processes, and properties of biological systems which have phylogenetic meaning are homologues. For Winther, homologues are the "objectively real characters" of phylogenetic analysis (Winther 2009, 131). In section 4.1.1 I will briefly review the definition of homology introduced previously and discuss Winther's reasons for thinking homologous characters are exclusively objective. Abstraction of such characters is the primary topic of Winther's (2009) research. He views abstraction as "central to the identification, individuation, and measurement of every character." (Winther 2009, 131) Section 4.1.2 explains abstraction and Winther's reasons for emphasizing its importance. Since Winther (2009) follows Rieppel and Kearney (2002) in the view that abstraction is a sort of recognition of similarity, he holds

that any such recognition is necessarily theory-laden. Section 4.1.3 explains Winther's claim that abstraction of taxonomic characters is always theory-laden.

Unfortunately, some abstracted characters are "misleading homoplasies," parts, processes, or properties of organisms which have no phylogenetic meaning and may be "irresponsibly reified." (Winther 2009, 131) Section 4.1.4 reviews the difference between homology and homoplasy, and explains Winther's concern that homoplasious characters can be mistaken for homologues. As a result of this concern, Winther emphasizes that a practical way to "distinguish irresponsibly reified characters from objectively real characters" is needed (Winther 2009, 131). Section 4.1.5 explains Winther's expectations for any method of doing so. In section 4.1.6 I briefly discuss the six criteria which Winther (2009, 131) describes as the "rigorous and empirically-based objectivity criteria for character analysis" already used by some cladists. Given that these criteria distinguish between homologues and homoplasies in the way he thinks is needed, Winther concludes that cladists have the means to attain "some objectivity in [their] ongoing systematic classification of the world of biological species and higher taxa." (Winther 2009, 131) I discuss in brief what this conclusion means for Winther in section 4.1.7, and the remainder of this chapter explains, via comparison with Richards' approach, what it means for the character individuation problem generally.

4.1.1 Homologues: Objectively Real Characters

Recall from section 2.2 that cladists divide shared traits into three categories: analogues, ancestral homologues, and derived homologues (Ridley 1993, 451).

If it was present in the common ancestor of the two species, it is a homology; if it was not (and therefore evolved convergently) it is an analogy. Homologies, in turn, divide into ancestral and derived homologies. An ancestral homology was present in the common ancestor of the two species, but evolved earlier and is also shared with other, more distantly related species; a derived homology first evolved in the common ancestor of the two species and is not shared with other more distantly related species. (Ridley 1993, 451-452)

Homologues, both ancestral and derived, are always present in the common ancestor of the two species who share that homologous character. Whether or not the homologues differ in form, function, or position, they are always different instances of the same character in ancestor and descendents. This evolutionary continuity among homologous characters makes homologues the only "phylogenetically informative" shared characters (Winther 2009, 133). We will discuss homoplasies, phylogenetically misleading shared characters, in section 4.1.4.

For Winther (2009), homologues are the objectively real parts, processes, and properties of biological systems. "Objectively real," here, takes on two meanings for Winther (2009, 131). In one sense, he takes 'objectively real' to mean existing in the mind-independent world.

> 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...a true cladogram...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). (Winther 2009, 138, footnote 6)

Godfrey-Smith (2003, 6) discusses this sort of objectivity as "a reality that exists regardless of how people conceptualize or describe it." In this sense, Winther (2009)

takes homologues to be the objectively real shared characters of evolution. In addition, Winther's (2009) 'objectively real' makes a distinction "between good and bad influences on belief." (Godfrey-Smith 2003, 228) However, Winther is not concerned with impartiality or lack of bias as Richards' (2003) was because he grants that "there is no 'view from nowhere' from which we can glean the true Natural System or Tree of Life." (Winther 2009, 138). The distinction Winther (2009) hopes to make is between shared characters which are rigorously tested and found to be homologous, and shared characters which are uncritically assumed to be homologous but never tested (Winther 2009, 133). Objectivity, for Winther (2009), is found with the application of a rigorous and empirically-based character abstraction process.

Godfrey-Smith's (2003) description of objectivity as the culmination of 'mindindependent existence' and 'good influences' summarizes the view used by Winther (2009) rather well.

> Beliefs are said to be formed objectively when they are caused by, or guided by, real things. Science counts as objective if it is a process in which belief and theory change are controlled by contact with real things in the world. (Godfrey-Smith 2003, 229)

Under this combined notion of objectivity, the only good influences on belief formation are mind-independent, "real things." (Godfrey-Smith 2003, 229) So the formation of beliefs is objective if it is influenced by—"caused by, or guided by"—the real world such that "belief and theory change are controlled by contact with real things." (Godfrey-Smith 2003, 229) For Winther (2009), a rigorous and empirically-based character abstraction procedure is one which is controlled by contact with the world. Characters are abstracted objectively when their abstraction is influenced by facts about evolutionary process, cladistic theory, and the specimens under study (Winther 2009). "Objectively real" characters are those which are parts, processes, and properties of "real biological systems," including evolutionary and developmental processes (Winther 2009, 130).

4.1.2 The Importance of Abstraction

Character abstraction is the main focus of Winther's (2009) research because, for him, the character problem boils down to the use of bad data due to irresponsible and careless character analysis. Winther presents it as follows:

> 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 the data matrices containing both morphological and molecular characters. 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. (Winther 2009, 139)

He discusses two possible solutions to this problem, the first focusing solely on increasing the *number of characters* and the second focusing solely on improving the *nature of characters*. The first approach presumes that the error from bad character data will balance out with large numbers of characters such that there is no need to restrict characters or worry about biological process when selecting character data (Winther 2009, 140). The second approach suggests that "we should not just abstract any possible character from our specimens; we need to use normative criteria." (Winther 2009, 141) Winther proposes that "the ideal is to combine the two: *the quality of the product of phylogenetic analysis is improved proportionately to the increase in number of good characters*." (Winther 2009, 141) He emphasizes but does not explain why "increasing

the sheer *quantity* of characters cannot be the entire solution to character analysis...we must also evaluate the *nature, quality,* and *content* of the data."¹² (Winther 2009, 141)

According to Winther, "bad characters" are a result of inadequate abstraction procedures. (Winther 2009, 142) Abstraction is the first stage of homology testing recognition of homologues via observation. Inadequate abstraction involves uncritical observation such that all similarities among specimens are counted as characters. Abstraction is adequate, for Winther, if some set of criteria ensure that only homologous characters are used (Winther 2009, 135). If characters which are not homologous are abstracted, then the second stage—testing for derived homology—will result in nonhomologous characters counted as derived homologues and result in inaccurate cladograms. "*Phylogenetic methods cannot fix bad data*," so the only way to solve the character problem is to improve the *quality* of the characters abstracted (Winther 2009, 139).

4.1.3 Abstraction is Always Theory-Laden

Abstraction of characters involves the recognition of similarity among properties of real biological systems. "In order to recognize similarity and thus the sharing of characters, a variety of abstraction processes must occur." (Winther 2009, 143) As an introduction to such processes, Winther describes four "modes of character abstraction:" abstraction away from character variation, abstraction of core properties, abstracted

¹² Winther (2009, 141) states that "we cannot be sure that character reifications will come out in the wash," as a reason for taking a closer look at the use of rigorous objectivity criteria during abstraction but does not provide a further explanation for this scepticism.

(homologue) identity, and abstraction by distortion of the specimen (Winther 2009, 144). Abstraction away from character variation involves ignoring "certain sorts of character variation." (Winther 2009, 143) The overall size of bones is a good example of variation to be ignored. Human bones are much larger than bat bones but abstraction of mammalian characters does not generally include coding of overall bone size. Abstraction of core properties involves focus on "the *essential properties* of parts or organisms." (Winther 2009, 143) An example which Winther gives for focus on core properties is the relative position of parts. The relative position of the mammalian forelimb bones is informative about which bone is which. Figure 4-1 shows the forelimbs of four different mammals. The ulna and radius are paired together and share an articulation with the *humerus*, for example.



Figure 4-1 Forelimb skeletal structure of a human, cat, whale, and bat; revised from Fig. 3.5 in Ridley 1993, 45

Abstracted identity involves recognition of the sameness of characters (homology) which is based on one-to-one correspondence of some part of one organism with that of another organism (Winther 2009, 143-144). Examination of the forelimbs in various mammals allows the recognition of the *humerus* (labelled in Figure 4-1) as a structure which has a one-to-one correspondence among mammals. Finally, abstraction by distortion is the use of perspective changes to make recognition of characters possible. "Tomography imaging of fossil skulls...can distort particular cross-sections to highlight relative position." (Winther 2009, 144) It is easier, for example, to recognise the *humerus* in each mammal when we look at all of the forelimbs from the same visual perspective.

Since these modes of recognizing homologues all involve recognition of 'sameness,' which could be compared to recognition of 'blueness,' they could be viewed as subjective in the same way that color perception is subjective—mind-dependent. In this way, the modes of abstraction could be subjective on Winther's view. Winther recognises that these modes could result in subjective character abstraction but emphasizes that critical analysis using objectivity criteria would ensure that abstraction is theory-laden rather than subjective (Winther 2009, 144).

If the various modes of abstraction follow the criteria to be detailed below, then the process is made objective and stops being perniciously subjective...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...of those objects. This abstraction is qualitative and structural. (Winther 2009, 144)

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For Winther, recognition of correspondence cannot be done without conscious omission of some properties and focus on others. "It would be impossible to eliminate theory from the abstraction process." (Winther 2009, 142)

Winther (2009, 142) goes on to describe three ways in which abstraction of characters is theory-laden. First, biologists come from diverse traditions and fields. The sorts of characters abstracted by cladists differ from those abstracted by evolutionary taxonomists, or pheneticists. Comparative anatomists, molecular geneticists, functional morphologists, and developmental biologists will each abstract different sorts of characters as well. Recall from section 3.1.5, for example, that molecular phylogeneticists are more likely to abstract molecular characters while comparative anatomists are more likely to abstract either skeletal characters or genitalia depending on the types of organisms they study (Richards 2003, 276). Second, diverse social contexts and individual insights provide background for various operational methods (for distinguishing, individuating, and measuring characters) and ontological assumptions (about what could possibly be a character). A taxonomist who was trained by specialists to value in depth study of characters, for example, will be more particular about what counts as a character and how to measure or individuate such characters. On the other hand, a taxonomist who was trained by broad-scale researchers to value having enough characters that "errors cancel out as noise" in their phylogenetic analyses will be less particular about what count as characters and how to measure or individuate them \cdot (Rieppel and Kearney 2002, 62). Finally, a cladogram may already be known such that characters may be abstracted to corroborate that cladogram. If such traditions, fields, methods, assumption, or preferred hypotheses influence character abstraction as Winther
(2009) proposes, character abstraction may be considered subjective for the same reason as the 'modes of abstraction.' These influences that make character abstraction "theoryladen" all seem to be mind-dependent influences, which are 'subjective' for Winther (2009).

The second way in which theory influences character abstraction is of greatest concern for Winther. He accepts that the operational methods and ontological assumptions involved in abstraction will make it theory-laden.

> 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. (Winther 2009, 144)

Winther emphasizes that abstraction is *always* theory-laden. He provides Kearney and Rieppel's (2006) discussion of the theory of pheneticists to establish this. As discussed in section 2.1, the pheneticists claim to have a theory-free approach to character individuation. These taxonomists classify organisms according to overall similarity. By recording as many characters as possible with no restrictions or preferences for type of characters, they group taxa by the greatest overall number of shared characters (Ereshefsky 2001, 61). Kearney and Rieppel (2006, 376) point out that even this type of approach is dependent on "the theory that morphological homologs can be discovered by ignoring anatomical complexity." Winther emphasizes his point with the discussion of Kearney and Rieppel's (2006) developmental character example as well. In order to count multiple developmentally correlated characters as independent characters, one would have "to *a priori* reject the hypothesis of developmental correlation." (Kearney

and Rieppel 2006, 375) "Regardless of how morphological and developmental characters are abstracted, we are always committed to a theory." (Winther 2009, 144)

4.1.4 Homoplasies: Not True Reflections of the World

Returning once again to our definitions of analogy and homology from sections 2.2 and 4.1.1, recall that analogies are characters shared by two taxa which are *not* also found in their common ancestor (Ridley 1993, 451). Birds' wings, for example, are analogous to flies' wings; 'wings' is a shared character of birds and flies but the common ancestor of birds and flies does not have wings; wings evolved independently— convergently—in these two taxa. Homoplasy is another term used to refer to this type of shared character. In the comparison of birds with flies, 'wings' is a homoplasious character, a shared character among birds and flies which is *not* also present in the common ancestor of these taxa.

For Winther (2009, 131), such characters "are not true reflections of the world," where "the world" refers to "the *empirically inaccessible yet true* Natural System or...Tree of Life." That is to say, homoplasies are not informative of evolutionary history. Winther goes so far as to call them "objects and properties of organisms that have no biological meaning." (Winther 2009, 131) Since homoplasies and homologies are both shared characters among taxa, homoplasious characters can look like homologous characters at first glance. For Winther, homologues are the only "objectively real" characters while homoplasious characters which are treated as homologues are "reified characters." (Winther 2009, 131)

4.1.5 The Need to Distinguish Homoplasies from Homologues

Given that there is a fact of the matter when it comes to the "Tree of Life" and only homologous characters are "phylogenetically informative,"—provide information about the evolutionary history of a group of taxa—homologues are the only characters that biologists should use as phylogenetic data (Winther 2009, 131).

> 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. (Winther 2009, 133)

The primary reason that a character matrix containing only homologous characters is ideal, is that homoplasious characters treated as homologues can result in inadequate—and historically inaccurate—cladograms (Winther 2009, 135). "Such cladograms...deviate significantly far from the real ones." (Winther 2009, 139) For this reason, character analysis requires some way to distinguish between homoplasious characters and homologues.

Winther maintains that careless and uncritical character analysis is the reason that homoplasious characters "corrupt" phylogenetic data (Winther 2009, 139).

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. (Winther 2009, 142)

In order to avoid error, Winther claims, "the nature of characters must be evaluated using objectivity criteria so that we can separate out primary homologies from reified characters." (Winther 2009, 140) According to Winther (2009), such criteria must do three things: be tested and refined through published sharing among a community of

biologists, guide processes of abstraction which are interactive with objects in the real world, and allow biologists to distinguish real from reified characters (Winther 2009, 143). For Winther, a set of criteria which does all these things will provide justification for the use of some characters and not others as "*good* or *proper* characters" for both present character analysis and future phylogenetic analyses (Winther 2009, 143).

4.1.6 Objectivity Criteria for Character Analysis

For Winther, proper characters come in three parts, (1) character-attributes such as 'has brown wings,' (2) character-parts such as 'wings,' and (3) character-variables such as 'wing color.' (Winther 2009, 145; following Colless 1985) Adequate homology claims, containing these character-parts, character-variables, and character-attributes, refer to parts, their characters, and their character-states respectively (Winther 2009, 145). Appropriate character-variables (characters) and character-attributes (character states) are entered in character matrices (Winther 2009, 145).

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...unless proven otherwise." (Winther 2009, 145)

Synapomorphies are derived homologues, shared by two taxa and their most recent common ancestor but no other common ancestors (Ridley 1993; Winther 2009, 145). Since cladistic methods assume that the shared characters in character matrices are homologues, objectivity criteria must be designed to ensure the selection of only homologous characters (Winther 2009, 146).

Winther's first three criteria are those implemented by Wiley (1981) for the recognition of homologous characters. The "relative positions" criterion is used to recognise the same part among taxa. Winther uses the mouth parts of two flies as an example (Figure 4-2). "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." (Winther 2009, 147)



Figure 4-2: A "sponging" fly (left) and a "piercing" fly (right) with relative position of homologous mouth parts numbered; revised from Wiley 1981, 132

The "special quality" criterion takes similarity of special structures and development into account (Winther 2009, 147). Winther (2009) and Wiley (1981) agree that the implementation of this criterion is most interesting when it disagrees with the relative position criterion. "Given that two structures correspond by positional criteria it is not at all unexpected that finer structure or similar ontogeny should be demonstrated for these structures." (Wiley 1981, 132) In cases where the two structures are in very different places or different positions, however, one can establish homology by looking at finer structures, embryology, and development. The shell of turtles and ribs of other vertebrates have very different positions and appearances, for example, but study of the embryology and development of turtles confirms that the homologues of vertebrate ribs in turtles are found within the shell (Burke 1989).

The final criterion Winther takes from Wiley (1981) is the "series of intermediate forms" criterion. This criterion is important in cases when the position, form, and function of the structures have all changed. Winther provides the comparison of the amphibian bones, *branchial*,¹³ *quadrate*, and *articular* to the three mammalian ear bones, *stapes, incus,* and *malleus* respectively as an example (Winther 2009, 148). While these bones would not pass the first two criteria, the series of intermediate positions, forms, and functions provide evidence that these are, in fact, homologues. "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." (Winther 2009, 148)

Winther's fourth criterion is taken from Patterson (1982;1988); the "conjunction" criterion states that "a given character cannot be homologous if two of its putatively mutually exclusive states are found in the same organism." (Winther 2009, 151) Given that the *articular* and the *malleus*, from our example above, are homologous characters, they are the same character with different forms, functions, and positions in different organisms. For this reason, the *articular* and the *malleus* cannot be found in the same organism. Angels are a common example of this criterion. If angels exist, having both wings and arms, this would disprove the putative homology of birds' wings with humans'

¹³ This is actually the *stapes* in both amphibians and mammals but Winther calls it the *branchial* in amphibians here.

arms. A pegasus or centaur would cause similar problems since it is commonly believed among taxonomists that the forelimbs of horses are homologous with the arms of humans and the wings of birds.

Winther takes his fifth criterion, "causal grounding," from Kearney and Rieppel. Designed to keep biologists in check to prevent the sort of unconstrained, biased delimitation of characters that Richards (2003) accuses them of, this criterion demands "the investigation of the causal structure underlying characters." (Winther 2009, 151) Winther (2009) agrees with Rieppel and Kearney (2007) that biologists need to evaluate characters within a causal context, including information about development, and function (Winther 2009, 152). Rieppel and Kearney (2007) use the 'vertebral column' of fish to illustrate such evaluations. The 'vertebral column' of sharks, sturgeon, and trout are all support structures for the body but develop quite differently (Rieppel and Kearney 2007, 100). A shark 'vertebral column' is formed by calcification of cartilage that "invades the notochord;" a sturgeon 'vertebral column' is formed by the four bony plates "applied to either side of the notochord;" and a trout 'vertebral column' is formed by the single bony structure that "replaces the notochord."¹⁴ (Rieppel and Kearney 2007, 100-101) Each type of 'vertebral column' is formed in a different way relative to the notochord (the developmental and evolutionary pre-cursor to vertebral columns), but a deeper investigation into the causal processes involved confirms that the 'vertebral column' is the same character in each case. "It is possible to identify somite re-

¹⁴ Keep in mind that vertebral columns are all segmented so when I say 'single structure' I mean 'single structure in each segment.' For a more complete and detailed description of these variations, see Rieppel and Kearney 2007, 100-101.

segmentation, sclerotome formation, cell migration and differentiation as the causal processes that result in the formation of vertebral columns." (Rieppel and Kearney 2007, 101) In this way, causal grounding allows for confirmation that the 'vertebral column' in each of the fish evaluated is homologous with the others.

"Inter-disciplinary communication" is the sixth and final criterion that Winther (2009, 152) proposes. He describes it as a "socially epistemic" criterion because rather than regulating abstraction of characters from the specimens under study, it regulates communication and critique of the other criteria. This criterion "promotes the sharing of meaningful causal and empirical information across scientific disciplines." (Winther 2009, 152) Notice that Rieppel and Kearney's (2007) 'vertebral column' example discussed above required an investigation into the embryological development of the 'vertebral column' in order to confirm that it is a homologue. Even though it has been widely accepted by comparative anatomists that all these instances of 'vertebral column' are the same character, comparative anatomy cannot explain *what* makes it the same. Furthermore, while embryology and developmental biology may have an explanation, a complete explanation may require other sub-disciplines of biology. The sharing of questions about what is the same in a particular homology as well as further investigation and critique of the answers provides 'causal grounding' at more points. For Winther, the more points of contact an investigation has with the real world (the more disciplines can provide causal grounding for it), the more objectivity that investigation has attained.

> 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 investigating *disciplines* (Winther 2009, 152)

In short, all areas of biology can contribute to character abstraction, and open lines of communication among biologists of various disciplines will result in the abstraction of good, homologous characters.

Winther proposes that together, these six criteria will allow for the justification of homology claims among taxonomic characters. The first four will "ideally mutually reinforce one another" while the fifth will deepen character analysis to resolve any conflicts (Winther 2009, 153). It is also Winther's expectation that the sixth criterion will allow for his whole set of objectivity criteria to be refined with continued use (Winther 2009, 153).

4.1.7 A Means of Attaining Objectivity

For Winther (2009, 143), objectivity in character abstraction requires that the abstraction process is interactive with the "real objects and properties under study,"— homologous characters in biological specimens—that it distinguishes real characters from reified ones, and that it is communally critiqued by biologists in various disciplines. His first five objectivity criteria are all interactive with the specimens under study as well as their parts, and properties. The sixth demands communal critique of the abstractions as well as the 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. (Winther 2009, 131)

Since objective character abstraction, for Winther (2009), requires that homologues and homoplasies are distinguished via interaction with the real world and critically evaluated by biologists of various disciplines, he concludes that his objectivity criteria provide the means to objective character abstraction.

4.2 Richards' (2002 and 2003) versus Winther (2009)

While Winther (2009) and Richards (2003) both discuss the character problem, they take two very different approaches. Winther (2009) points out that Richards (2002 and 2003) takes on a contrastive approach, making distinctions and drawing lines that Winther disagrees with. I review Winther's discussion of these in sections 4.2.1 and 4.2.2. Winther (2009) also mentions, but does not discuss explicitly, the optimistic approach he takes in trying to find and expand on objectivity in current phylogenetic methods while Richards (2003) focuses on sources of subjectivity in those same methods. I will discuss this subjectivity-objectivity contrast in section 4.2.3.

4.2.1 Algorithms versus Background, Tradition, and Training

Winther (2009) contrasts his project with Richards' (2002) on the basis of their expectations for adequate phylogenetic inference. While Winther (2009) accepts that character abstraction is theory-laden but, nevertheless, able to be objective, Richards (2002) takes background information, tradition, and training to be subjective sources of character ascriptions which are in opposition to algorithmic rules (Winther 2009, 154). "According to Richards, there is no "algorithm" or rule with which to individuate characters." (Winther 2009, 154) Richards' (2002, 2) expectations for adequate

character individuation involve the application of an algorithm, a decision procedure which unequivocally leads every researcher who applies it to the same decision. Winther points out that "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." (Winther 2009, 154) Winther (2009) rejects this distinction, however, and suggests a set of objectivity criteria for adequate character abstraction which take into account background information, tradition, and training.

4.2.2 Non-Scientific Data Sources versus Scientific Data Sources

Winther (2009) also contrasts his project with that of Richards (2003). Winther (2009) takes Richards (2003) to be contrasting non-scientific sources of evidence with scientific sources of evidence.

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 nonscientific background information, tradition, and training. (Winther 2009, 154)

Winther argues against Richards' (2003) contrast even more vehemently than he did the

algorithm-background contrast of Richards (2002).

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. (Winther 2009, 154-155) Winther (2009) cautions philosophers against making a sharp distinction between scientific and non-scientific factors or claiming that the lack of a "single, rigid, "algorithmic" procedure" is enough to deem a method subjective (Winther 2009, 155).

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, operation methods, and ontological assumptions. (Winther 2009, 155)

4.2.3 Subjective Individuation versus Objective Abstraction

Richards (2003) focuses on character individuation as a source of subjectivity in cladistic method while Winther (2009) focuses on character abstraction as a source of objectivity. Since cladists lack a principle of character individuation which can identify and individuate characters adequately (by Richards' standards), both character individuation and phylogenetic inference may be subjective or arbitrary (Richards 2003). On the other hand, Winther (2009) points out that the objectivity of phylogenetic inference depends on that of the character data used. For this reason, he determines which criteria cladists are already implementing to ensure that their data is objective and improves the criteria set by adding a causal grounding criterion and an inter-disciplinary communication criterion. While Richards (2003) finds subjectivity in cladistic method, Winther (2009) finds objectivity.

While 'subjective' and 'objective' are generally considered to be in opposition, the various meanings of each term make it rare that they are, in fact, direct opposites. Godfrey-Smith (2003, 6) distinguishes between two meanings of 'objectivity,' and their matching notions of 'subjectivity'. The mind-independent existence—'objectivity'—of water may be contrasted with the mind-dependent existence—'subjectivity'—of color, while the impartial or unbiased 'objectivity' of simple addition may be contrasted with the predisposed or biased 'subjectivity' of artistic analysis (Godfrey-Smith 2003, 228-229).

Along with taking different approaches to the character individuation problem, Richards (2003) and Winther (2009) use different meanings of 'objectivity' and 'subjectivity'. As discussed in section 3.1.1 Richards (2003), takes 'subjective' to mean biased. Winther (2009) takes 'objective' to mean influenced by mind-independently real objects (discussed in section 4.1.1). As Winther (2009) points out, Richards (2003) seems to consider "background information, tradition, training, operation methods, and ontological assumptions" to be sources of subjectivity in character individuation (Winther 2009, 155). Winther (2009) considers these same factors to be sources of objectivity for character abstraction when appropriately combined to connect abstraction to the real world (Winther 2009, 154-155). This variation in use of 'objective' and 'subjective' is worth keeping in mind during any comparison of Richards (2003) and Winther (2009). They are both focused on the influences of taxonomic beliefs but Richards (2003) considers only theory-free, algorithmic influences to be good while Winther (2009) wants influences which account for the fact that they are unavoidably theory-laden via realworld connection.

4.3 Winther's Optimistic Conclusion

Winther (2009) concludes by emphasizing the importance of the causal grounding criterion, as well as the inter-disciplinary communication criterion, for character abstraction. He thinks that "a socially-organized complex science need not be seen as conflicting with a science seeking objective empirical knowledge." (Winther 2009, 156) It is to promote this view of taxonomy that he includes his fifth and sixth criteria. While the first four criteria importantly outline how homologues can be recognised and distinguished from other shared characters, the causal grounding criterion provides justification for our preference of homologues (Winther 2009, 155).

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...in short, sameness of (potentially phylogeneticallyconstrained) cause explains sameness of characters. (Winther 2009, 155)

Rieppel and Kearney (2007, 101) explain this notion using 'the vertebral column' of vertebrates. 'The vertebral column' takes on different forms among vertebrate species, and while there is similarity among the different instances of 'the vertebral column,' giving a single description of it is impossible (Rieppel and Kearney 2007, 101). However, delving into the developmental processes for each instance can provide insight into common cause. Since "underlying causal relations of development...determine the extension of the natural kind term 'vertebral column'," identification of the causal processes involved with the formation of 'the vertebral column' allows the justification of homology claims about instances of 'the vertebral column' of vertebrates (Rieppel and Kearney 2007, 101).

Winther (2009) also emphasizes the importance of the inter-disciplinary communication criterion which directly promotes a socially interactive view of objective science.

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. (Winther 2009, 156)

While the other five criteria are products of sharing and critique, this sixth criterion promotes the continuation of inter-disciplinary communication in the application and refinement of Winther's (2009) abstraction process. Inter-disciplinary communication allows Winther's (2009, 157) objectivity criteria to be "neither absolute nor final," because with ongoing testing and criticism, the criteria may need to change. He suggests that they will need further elaboration and continuous criticism in order to remain a robust set of criteria for character abstraction (Winther 2009, 157). According to Winther (2009), cladists "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."

4.4 Winther's Approach and the Character Individuation Problem

Winther (2009) optimistically argues that cladisitc character analysis is objective and takes his objectivity criteria to provide a solution to the character problem as he defines it. The character *individuation* problem, however, is another matter. Section 4.4.1 explains that Winther (2009) discusses a general character problem but fails to examine the character *individuation* problem that Richards (2003) and I are concerned with. While Winther (2009) takes himself to be arguing against Richards (2003), his argument is against a generalized version of Richards' (2003) pessimistic conclusion. This seeming avoidance of the character individuation problem is discussed in section 4.4.2. Unfortunately, restricting taxonomic data to homologous characters neither solves nor avoids the character *individuation* problem. Section 4.4.3 explains how this problem remains in spite of Winther's found objectivity in character analysis.

4.4.1 Quality vs. Quantity: The Number of Good Characters

Returning, briefly, to the explanation Winther (2009) gives of the character problem and its possible solutions, it becomes clear that he is not discussing the character *individuation* problem.

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.* (Winther 2009, 133)

Winther (2009) presents this general problem—that inadequate character sets produce problematic cladograms—but he does not discuss the individuation part of the problem that the same structure can be individuated as either one or multiple characters. Recall from sections 2.4 and 3.1.4 that the three bones of the mammalian ear could be individuated as a single three-ear-bones character or as three individual characters. Since phylogenetic inference uses the number of shared characters to select a cladogram, the outcome of the analysis can be determined by whether a single character or multiple characters are counted for any given structure.

Winther (2009) presents two possible solutions to the general character problem: an increase in the sheer quantity of characters, or an increase in the quality of characters. For Winther (2009), the ideal solution is an increase in the quantity of quality characters. He explains how an increase in the sheer number of characters fails to solve the problem and moves on to explain that quality of the characters is all important. As we discussed in section 4.1.1, Winther's (2009) good quality characters are exclusively homologous characters—different instances, forms, and functions of the same character, shared by two species and at least their most recent common ancestor. These characters are contrasted with homoplasious characters, characters which are not the 'same character' but mere convergently evolved similarities.

Winther's (2009) ideal solution to the general character problem is to increase the number of homologous characters while decreasing the number of homoplasious characters. Sets of high quality characters from objectivity guided character abstraction will, given "subsequent high quality phylogenetic analysis," produce good cladograms (Winther 2009, 133). However, Winther (2009) does not say anything about how variation in the number of characters counted for each homologue may affect phylogenetic analysis, making it apparent that *individuation* of characters is not Winther's (2009) focus.

4.4.2 Winther's Approach to Richards' Individuation Problem

Winther (2009, 157) takes himself to be arguing that "we need not accept Richards' overly pessimistic, subjectivist view of character analysis." This is not, however, just because Winther takes an optimistic, objectivity focused approach to character abstraction. He also understands Richards' argument to contrast real characters with merely abstracted characters.

> 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...because all good characters are *both* real and abstracted. (Winther 2009, 157)

Winther takes Richards to be arguing that subjectivity in phylogenetic inference results from arbitrary abstraction of characters rather than individuation of "real characters" and argues against this contrast. Since, for Winther (2009), "all good characters are *both* real and abstracted," he suggests that the appropriate contrast for cladistics is between "theory-laden, robustly real characters" and "uncritically reified" characters. (Winther 2009, 157)

Winther (2009) thinks that we should be concerned about subjectivity in cladistics resulting from subjective character analysis but that use of his objectivity criteria for abstraction will prevent both. That is, if characters were arbitrarily selected as Richards (2003) proposes, there would be a character problem. Since, for Winther (2009), characters are deliberately selected for their homology, there is nothing arbitrary about character analysis; problems only arise when cladists carelessly assume homoplasious characters to be homologues, and Winther's (2009) objectivity criteria reduce the

occurrence of such mistakes. In this way, Winther (2009) fails to consider the character *individuation* problem as Richards' (2003) and I present it.

4.4.3 Character Individuation and Winther's General Solution

Setting aside any epistemic concerns about how effective Winther's (2009) six objectivity criteria for abstraction actually are, let us assume that some set of criteria can do the job. That is, we assume that some set of objectivity criteria, *O*, can be applied during character abstraction to ensure that only homologous characters are included in any character set used for phylogenetic inference. The question then becomes: can the application of *O* avoid or solve the character *individuation* problem? If there is only one way to individuate homologous characters then the application of *O* solves the character *individuation* problem. If, however, there are multiple ways to individuate homologous characters, character *individuation* remains a problem even with "objective" character abstraction.

Winther's 'relative position' criterion can be used to identify the same part in multiple taxa when a part has the same position relative to other common structures. The forelimb skeletal structure of mammals (Figure 4-1), for example, includes the skeletal hands of humans and the skeletal paws of cats which have the same relative position with respect to the wrist bones (carpals) of their respective forelimbs. Similarly, each bone within the hands of humans can be mapped to a bone within the paws of cats. Based on relative position we could homologize the hand of humans with the paws of cats and individuate the hand-paw as a single character with a character state for humans and a character state for cats. We could also homologize each of the five digits with the same

relative position and individuate them accordingly. The digit numbered '5' on the human forelimb in Figure 4-1 and the digit numbered '5' on the cat forelimb would be a single character with two character states (one for cats and one for humans). Under this individuation each of the other four digits would be a separate character with two states in the same way. The first individuation had one character with two states while the second individuation had five characters with two states each. While there are still more ways to individuate this particular group of bones, we just need more than one for the individuation problem to take hold. It seems that even if the relative position criterion successfully picks out homologous structures, there are multiple ways to individuate the homologized structures.

As we discussed in section 4.1.6, the 'special quality' criterion is most interesting in cases when the 'relative position' criterion fails to identify the homology. For this reason, let us return to the turtle shell example. Recall that a developmental study of the turtle shell reveals that it contains the turtle's ribs—which are homologous to the ribs of other vertebrates, including humans (Burke 1989). Given this homology established by the 'special quality' criterion, we can individuate a single 'vertebrate ribs' character with two character states, one for the turtle position (outside of the limb girdles) and one for the human position (inside the limb girdles). Following Richards' (2003) reaction to the individuation of the 'spiny coat' of the spiny anteater, we could also individuate each rib separately or group them into sections to individuate multiple characters for the vertebrate rib homology. While the 'special quality' criterion is great at identifying those hard-to-see homologues, it also allows for multiple individuations of those homologues.

The 'intermediate forms' criterion can also establish homology for hard-to-see homologues. The homology of the jaw bones of amphibians with the ear ossicles of mammals is a wonderful example of a homology that is easily established by showing its intermediate forms. As Richards (2003) points out, however, there are multiple ways of individuating these homologous characters. We can individuate each bone separately with a state for each stage under study or we can individuate portions of each bone separately. For example, the portion of the stapes closest to inner ear could be individuated as its own character with its various 'intermediate forms' as character states. This 'intermediate forms' criterion, thus, allows multiple character individuations of the homologues it identifies.

The same problem arises when the 'conjunction' criterion is applied. Recall that the discovery of an angel would disprove the putative homology of the forelimbs of humans (arms), and birds (wings) because an angel is a single organism having two of the supposed mutually exclusive states of the vertebrate forelimb. Since the angel's arm and the angel's wing would both contain a *humerus*, *radius*, and *ulna* (the three large bones in the vertebrate forelimb), two instances of each would be present in the angel. So the angel could have one character with two states that are supposed to be mutually exclusive or it could have three. In this way, there would be multiple ways to individuate the putative homologues even as they are being disproven.

Recall from section 4.1.6 that the 'causal grounding' criterion delves into the function and development of a putative homology in order to establish the causal processes which result in the various instances of that homology. Rieppel and Kearney (2007, 101) use the 'vertebral column' as an example, establishing its homology in

sharks, sturgeon, and trout by identifying the "somite re-segmentation, sclerotome formation, cell migration and differentiation as the casual processes that result in the formation of vertebral columns." Individuation of the 'vertebral column' is not explicitly discussed but they do treat it as a single character, throughout their discussion. So we could individuate the 'vertebral column' character as the single product of the above listed causal processes with different character states accounting for variation in the development of the 'vertebral column' with respect to the notochord in sharks, sturgeon, and trout. Since the 'vertebral column' is formed by four causal processes (somite resegmentation, sclerotome formation, cell migration, and cell differentiation), each of the causal processes could be individuated separately as characters with states accounting for the variation in each of the fish under study. In this way, the 'causal grounding' criterion can allow for multiple individuations of the same homology.

The 'inter-disciplinary communication' criterion can be viewed as the implementation of the 'causal grounding' criterion by various biological disciplines and comparing the results. If no discipline can disprove a homology claim and those who evaluate the claim find only evidence to corroborate it, we can be justified in including that homology in our character sets. How many characters that homology is composed of, however, is still up for debate. If the causal processes, genetics, molecules, anatomy, physiology, biochemical mechanisms, and function of the 'vertebral column' are all known and can be used to establish its homology among vertebrate taxa, it is still possible that each discipline will individuate a different set of characters for the 'vertebral column.' The number of vertebrae may be individuated as a character with multiple states by the anatomist while the geneticist individuates the various genes and the parts of

the vertebral column each gene codes for. The more disciplines that are communicating, the more individuations are possible for each established homology.

Winther's six criteria each allow for multiple individuations of the homologues they identify. Homology can occur on multiple levels, as we have seen most clearly in the forelimb examples where the arm of humans is homologous with the wings of birds and the bones which comprise the human arm are homologous with the bones which comprise the bird wing. Given this fact about homology, it seems that any set of criteria which only strives to establish homology will fail at solving or avoiding the character individuation problem. Unless the criterion guides the individuation of these homologues, Richards' (2003) pessimism is still able to take hold, the individuation of characters could still be done arbitrarily or subjectively. While Winther's objectivity criteria (or some set of objectivity criteria) can differentiate homologous characters from homoplasious characters, it is still possible that they will allow for arbitrary or subjective individuation. So even if we are restricted to abstraction of homologous characters by the set of objectivity criteria, *O*, the character *individuation* problem remains a problem.

Chapter Five: An Approach Toward a Solution

In this chapter, I review the character individuation problem, how it arises and why it is of concern to cladists. I, then, review the contrasting approaches Richards (2003) and Winther (2009) take to the problem and what each philosopher concludes about the problem. Finally, I consider what we have learned through our discussion of these accounts and what might be involved in a satisfactory solution to the character individuation problem.

5.1 A Review of the Problem

In section 2.4 I discussed two examples of characters which can be individuated in multiple ways, the three ear ossicles of mammals and the hindlimb of *Pachyrhachis*. While both of these are examples illustrating the topic of this thesis—the character individuation problem—the first does not seem to cause cladists any practical problems while the second has perpetuated debate about the origin of snakes for over thirty years. In section 5.1.1 I briefly review these two examples and the character individuation problem generally. Then in sections 5.1.2 and 5.1.3 I review Richards' (2003) and Winther's (2009) approaches to the problem, respectively.

5.1.1 Ear Ossicles, Hind Limbs, and the Individuation of Characters

Recall from section 2.4 that having three ear ossicles is a derived homologue of mammals. That is, platypus, humans, and their most recent common ancestor share the state 'three' for the 'number of ear ossicles' character. However, if we zoom in on

mammals in order to compare cats with humans, the same 'three ear ossicles' character is an ancestral homologue. It is shared by cats, humans, their most recent common ancestor, and more distant ancestors (Ax 1987, 144). In this way, the characters which are of interest to cladists for phylogenetic inference—derived homologues—change depending on the level of comparison (Ax 1987, 144; Sober 1988, 35). Importantly, however, there are multiple ways to individuate the ear ossicle characters and their states at each level of comparison.

The *columella auris* (or *stapes*)—the single ear ossicle found in non-mammalian tetrapods as well as mammals—has a very different shape in mammals than it does in other tetrapods (Ax 1987, 145). For this reason, it could be individuated as its own character with its different shapes counted as different character states. Similarly, we could separately individuate the two jaw bones of non-mammalian tetrapods, the *quadrate* and the *articular*, which are homologues of the remaining two ear ossicles in mammals, the *incus* and the *malleus* respectively (Ax 1987, 145). The '*quadrate-incus*' character and the '*articular-malleus*' character, would each have multiple character states to designate its shape variation. If we maintain the same number of possible states under this character individuation as we had for the 'one' versus 'three' 'number of ossicles' character, having a mammalian state and non-mammalian tetrapod state, platypus and humans share three characters with their most recent common ancestor. For this individuation of tetrapod ear ossicles, then, there are three derived homologues uniting mammals rather than just one.

Ax (1987, 146) makes it clear that the original individuation, 'one' versus 'three' ear ossicles, is "no longer of any use" if we are comparing types of mammals or species within one of the types of mammals (humans compared to cats) because under such phylogenetic analyses all the organisms have the same character state for the 'number of ear ossicles' character. As was discussed by both myself in section 2.4 and Richards (2003), however, Ax (1987) does not mention the use of an individuation like the 'quadrate-incus'-'articular-malleus' individuation articulated above to represent the transition from one to three ear ossicles. So it is not clear whether the transition from one to three ear ossicles in the evolutionarily novel ancestor of mammals should be represented as one evolutionary change or three. I will review the problem this ambiguity presents once we are also reacquainted with *Pachyrhachis*.

In section 2.4 I introduced *Pachyrhachis*, a fossil snake with the head of a python and the limbs of a lizard. While it may sound like a breast from Greek mythology, it is a quite real problem for cladists. *Pachyrhachis* has many features in common with present day Macrostomatan snakes (large-mouthed snakes like Pythons) and also exhibits welldeveloped hind limbs (Rieppel et al. 2003, 537). Proposed character sets for this organism have varied substantially. Some emphasize the highly mobile skull and jaw that *Pachyrhachis* has in common with Macrostomatans and some emphasize the relatively well-developed hind limb which differentiates it from all snakes.

When the character set for *Pachyrhachis* exclusively includes cranial characters abstracted from the head and jaw—the resultant cladogram shows *Pachyrhachis* as a Macrostomatan snake (Tchernov et al. 2000, 2012; Rieppel et al. 2003, 553). This placement is labelled as *Pachyrhachis A* in Figure 5-1. When characters behind the head, post-cranial characters, are also included and the hind limb is counted as a single character in the character set for *Pachyrhachis*, the resultant cladogram includes it as the "sister-group to Macrostomatans" within snakes (Zaher 1998, 2; Zaher and Rieppel 2002, 108; Rieppel et al. 2002, 553). This placement of *Pachyrhachis* is labelled in Figure 5-1 as *Pachyrhachis B*. If the pelvic girdle and hind limb elements are all counted as separate characters, *Pachyrhachis* is shown to be a transitional form between lizards and snakes (Caldwell and Lee 1997, 708; Lee and Caldwell 1998, 1544; Caldwell 2000, 188; Rieppel et al. 2003, 553-554). This placement is shown (without the specific lizard groups involved in the lizard to snake transition hypothesized) in Figure 5-1 as *Pachyrhachis C*.



Figure 5-1 Combination of cladograms in Figures 2-7, 2-8, and 2-9 showing the most parsimonious placement of *Pachyrhachis* when the character individuation includes (A) only cranial characters, (B) cranial, post cranial, and a single hind limb character, or (C) cranial, post cranial, multiple hind limb and pelvic girdle characters. Note that this figure does not show a true cladogram and that these hypotheses each differ by the 'Other Squamates' included and their placement with respect to snakes.

As discussed in section 2.4, cladists concerned with the origins of snakes and the phylogenetic placement of *Pachyrhachis* are well aware that the character set used for comparison of Pachyrhachis with other organisms determines which cladogram is most parsimonious. They debate at length how many and which parts of the skull and hind limb are appropriate to code as characters (Caldwell and Lee 1997; Lee and Caldwell 1998; Zaher 1998; Caldwell 2000; Zaher and Rieppel 2002; Tchernov et al. 2000; Rieppel et al. 2003; Rieppel and Kearney 2007). 'Splitting' part of the specimen into a large number of characters while 'lumping' another part of the specimen into fewer characters greatly affects the outcome of phylogenetic inference (Rieppel and Kearney 2007, 105). Individuating characters to emphasize the head and jaw of Pachyrhachis while understating the hind limb, results in a most parsimonious cladogram showing Pachyrhachis as a Macrostomatan snake. Conversely, if the well-developed hind limb of Pachyrhachis is 'split' and the cranial features are 'lumped', Pachyrhachis is most parsimoniously classified as a transitional from between lizards and snakes (Rieppel and Kearney 2007, 105). Since it is up to each cladist to determine the most appropriate character individuation for her investigation, each such individuation may contain a different character set for Pachyrhachis. Given this variability in character sets and the fact that each character individuation may result in a different most parsimonious classification, there does not appear to be only one most parsimonious classification for Pachyrhachis (Richards 2003; Rieppel and Kearney 2007, 105).

In both the mammalian ear ossicle and *Pachyrhachis* cases, there are multiple ways to individuate characters into a character set, and in the case of *Pachyrhachis* the consequence is multiple, conflicting, most parsimonious classifications involving *Pachyrhachis*. Since the evolutionary history cladists are attempting to reconstruct using phylogenetic inference is history, however, it is assumed that it actually occurred via some set of events and that a reconstruction of that history will involve mapping the order of those particular branching events. This implies that only one reconstruction can be historically accurate. In the *Pachyrhachis* example, then, only one classification can be a historically accurate mapping of evolutionary history.

While individuation of the ear ossicles themselves does not cause a problem with multiple classifications as the *Pachyrhachis* example does, it is still disconcerting that there is not always an explicit reason for cladists to 'split' or 'lump' such characters. New developmental and paleontological research suggesting that the ear ossicles may have actually evolved multiple times within mammals could lead to such individuations causing problems (Meng et al. 2011). 'Lumping' the middle-ear complex into a single character may maintain the mammalian classification that had been accepted before new research put it into question; on the other hand, 'splitting' the middle-ear bones as well as enough supporting structures of the ear could lead to a classification with those mammals lacking the middle-ear complex all grouped together as 'basal mammals' in spite of the differences between the marsupials, placental mammals, and monotremes among them. Since number of characters was used to select the original accepted classification of mammals among other tetrapods, it is just a matter of 'splitting' or 'lumping' certain characters *enough* to cause the selection of a different hypothesis.

More precisely, selection of a correct reconstruction by cladists is based on the use of parsimony; this assumption that evolutionary change is improbable allows cladists to pick out the reconstruction which involves the least number of changes as being the best phylogenetic inference; evolutionary change is quantified by comparing homologues and designating differences between homologues as different states of the same character. So cladists can quantify change in the number of ear ossicles by assigning 'one' as the state of the 'ossicle number' character for one organism while assigning 'three' as the state of the same character in a different organism. Designation of these differences and individuation of the homologues into characters can be done in multiple ways (as our ear ossicle and hind limb examples demonstrate), resulting in multiple character sets. So quantification of evolutionary change (individuation of characters) can be done in multiple ways and the selection of the best phylogenetic inference is dependent on these individuations.

5.1.2 Richards' (2003) Approach: Subjective Individuation

While I have explained that there is sometimes a lack of explicit reasons given for individuating characters in one way over another, Richards (2003) goes several steps farther. He suggests that no explicit reasons given by cladists are unequivocally decisive and character individuation, as a result, is either arbitrary or subjective. That is, rather than using an unequivocal individuation rule or principle, cladists can individuate characters arbitrarily—with no justification—or they can individuate characters in favour of a particular hypothesis; cladists could, for example, 'split' the hind limb into fifteen characters to fit *Pachyrhachis* into a particular transition story for the evolutionary origin of snakes. If characters are arbitrarily individuated then cladists are not justified in claiming the hypothesis selected is 'most parsimonious.' Similarly, individuating

characters with a particular outcome in mind may make the 'most parsimonious' hypothesis more a reflection of that preferred outcome than of evolutionary history.

Richards (2003) takes the possibility of subjective or arbitrary classifications to be the pressing character problem; he suggests that if cladists were to use an 'unequivocal principle of character individuation,' such arbitrary or subjective individuation and the resultant unjustified or biased 'most parsimonious' hypotheses could be avoided. According to Richards (2003), however, cladists do not have such an 'unequivocal principle of character individuation.' He comes to this conclusion because every principle used by cladists allows for multiple individuations of the same trait into characters. Richards (2003) uses the three ear ossicles example to illustrate this fact for every potential principle he considers. The 'three ossicle complex' is just as *separable* from other morphological elements as is each ear ossicle independently. Similarly, the independent ossicles can be individuated separately by *function* within the complex just as readily as the 'three ossicle complex' can be individuated as a *functional* complex. The *developmental* pathways of each ossicle can be individuated just as those of the whole complex; and obviously both the three ear ossicles complex and each ossicle within the complex can be *perceived* and *communicated* among cladists (and philosophers) or they would not make a very good illustrative example.

For Richards (2003), selection of one way to individuate characters over another way by anything other than an 'unequivocal principle' is either an arbitrary selection or a subjective selection. Similarly, allowing for multiple parsimony outcomes and selecting a hypothesis independently of an 'unequivocal principle' is arbitrary or subjective selection of that hypothesis. Since objectivity, for Richards (2003), requires immunity to subjective influence, phylogenetic inference without an 'unequivocal principle' directing each step fails to be objective. Given that the application of parsimony would be 'unequivocal' if it weren't for subjective character individuation, Richards (2003) concludes that cladists (and probably all taxonomists) need a whole new character concept and individuation scheme which is 'unequivocal'.

5.1.3 Winther's (2009) Approach: Objective Abstraction

Winther (2009) takes quite a different approach to this problem, suggesting that the pressing problem is identification of homologies—the 'real' parts, properties and processes of evolutionary history—and disproval of the 'reified' homoplasies which can be mistaken for homologies if taxonomists are uncritical. For Winther, a character abstraction process which distinguishes between homologues and homoplasies in this way is prior to character individuation. Before taxonomists can individuate, and measure characters (homologues), they must be abstracted from the specimens under study; and for Winther, it is the quality of this abstraction process that determines the quality of the taxonomic data.

For Winther, objectivity is required for quality character abstraction, in the sense that the real—meaning objective for Winther—parts, processes, and properties of biological systems should influence abstraction. While incorporating the influence of real parts, processes, and properties involves incorporating theory in many ways, the theory-ladenness of abstraction does not diminish its quality, according to Winther. He argues that abstraction is necessarily theory-laden but that it need not be subjective if both the homologies and the process of identifying those homologies undergo robust empirical testing.

He proposes that abstraction could be objective if six criteria are implemented during the abstraction process. The first four criteria establish homology claims by testing the 'relative position,' 'special quality,' 'intermediate forms,' and 'conjunction' of the proposed homologues respectively. The fifth criterion provides 'causal grounding' to the homology claim, studying the development of the proposed homologue to find its causal processes. The sixth criterion promotes 'inter-disciplinary communication' for the ongoing criticism and testing of the other five criteria. These six 'objectivity criteria' are, thus, designed to test homology claims, increasing the number of homologues and reducing the inclusion of homoplasies in taxonomic data sets.

Winther (2009) proposes these six criteria as a response to Richards' (2003) claim that biologists do not have an unequivocal principle of character individuation.

Our contrast in cladistics should not be one between really real characters and purely "abstracted" characters, as Richards argues...because all good characters are *both* real and abstracted. Instead, our contrast should be between theory-laden, robustly real characters *and* uncritically reified ones. (Winther 2009, 157)

Winther's (2009) criteria show that cladists are not individuating just any characters or characters which suit their goals, as Richards (2003) suggests. Rather, cladists are abstracting real—homologous—characters in a necessarily theory-laden and critical way. Unfortunately, while Winther's (2009) criteria may distinguish homologues from homoplasies, they do not succeed in addressing the character individuation problem. Recall from section 4.4.3 that the wing of a bird is homologous with the arm of a human and the *humerus* of the wing is homologous with the *humerus* of the arm; whether to individuate the wing and arm as a single character with two states or the *humerus* and other bones within the wing and arm as individual characters with two states, is not answered by the verification that they are homologous. Although Winther (2009, 157) tries "to argue that we need not accept Richards' overly pessimistic, subjectivist view of character analysis," the character individuation problem is still a problem under his approach.

5.2 An Approach Toward a Solution

Taking important points from Richards (2003), Winther (2009), and the discussions of them in Chapters Three and Four respectively, I propose that an approach which combines their concerns is most likely to lead to a solution to the problem. I agree with Richards (2003) that cladists need an 'unequivocal principle of character individuation' whether it takes the form of a single principle or a set of criteria. I suggest, however, that such a principle or set of criteria would need to be context sensitive. As I suggest below, a principle of character individuation must take the scope of phylogenetic analysis into account in order to support the phylogenetic goal of mapping out the branching events from evolutionary history. Also, agreeing with Winther (2009) to some degree, any reconstruction of evolutionary history should take into account the evolutionary processes and mechanisms which allow evolution to occur in the first place. An 'unequivocal principle of character individuation' which takes these and other aspects of context into account would be a good start to solving the character individuation problem.

5.2.1 An Unequivocal Principle of Character Individuation

According to Richards (2003), a satisfactory principle of character individuation must function to support the goal of phylogenetic inference—"the reconstruction of the branching order of the evolutionary past." (Richards 2003, 278) In order to determine what sort of principle would be able to support such a goal, section 3.2.1 distinguished two possible interpretations for Richards' (2003) satisfactory principle of character individuation. One interpretation was that this satisfactory principle is a *principle of unequivocal character individuation*, a principle which dictates the same, unambiguous individuation of characters under *any* taxonomic input; the other suggested that the satisfactory principle is an *unequivocal principle of character individuation*, a principle which unambiguously dictates a single individuation of characters for *each* taxonomic input.

As we discussed in section 3.2.1, an *unequivocal principle of character individuation* is distinct from a *principle of unequivocal character individuation*. A *principle of unequivocal character individuation* specifies the same individuation for a given feature under any circumstance. Under such a principle, if the 'three ear ossicles' of mammals counts as a single character with three states in one character set, it must be a single character with three states in every character set. Similarly, if the 'welldeveloped hindlimb' of *Pachyrhachis* is individuated as a single character under such a principle, it must be individuated as a single character in every character set. Since always individuating the hindlimb as a single character would disregard differences within the limbs of organisms, this identical individuation for a given feature under any circumstance does not function to support the "reconstruction of the branching order of the evolutionary past." (Richards 2003, 278)

An unequivocal principle of character individuation, on the other hand, must unambiguously specify a single outcome for each *input*. Under this type of principle, any time the input changes, the individuation of characters for the output character set also changes. The 'three ear ossicles' of mammals could be individuated as a single character with two states in one case and three separate characters with two states each in another case. Similarly, an unequivocal principle of character individuation would allow that the 'well-developed hindlimb' of *Pachyrhachis* be individuated as a single character in one case and multiple characters in another. For example, the hindlimb could be individuated as a single character such that the absence of the hindlimb in limbless snakes would be accounted for but not be exaggerated by the 'absence' of multiple characters; the hindlimb could also be individuated as multiple characters so the differences between tetrapod knee joints would be accounted for. This adjustment for changes in input allows the *unequivocal principle* to support the goal of phylogenetic inference, making it a satisfactory principle of character individuation. From this analysis and the analysis of Richards' (2003) satisfactory principle in section 3.2.1, it can be concluded that cladists need an 'unequivocal principle of character individuation'—a principle which unambiguously specifies a single outcome for each taxonomic input.

5.2.2 Taking the Scope of Phylogenetic Analysis into Account

One way in which the individuation of characters can vary is by the scope of the particular phylogenetic analysis for which the individuation is being done. When taxa
that are more closely related to one another are compared, the scope of the phylogenetic analysis is narrower. Conversely, when taxa that are more distantly related to one another are compared, the scope of the corresponding phylogenetic analysis is broader. The phylogenetic comparison of two placental mammals, humans and cats for example, is narrower in scope than the phylogenetic comparison of a placental mammal and a monotreme, humans and platypus. If a non-mammalian tetrapod like salamanders was added to either of these analyses, the scope would be broader. The addition of an invertebrate like lobsters would make the resulting phylogenetic analysis broader still. When the diversity of organisms included differs among phylogenetic analyses, the individuation of characters may need to differ as well.

Ax (1987) discusses the scope of phylogenetic analyses in order to illustrate the relativity of ancestral and derived homologues. "Whether a particular agreement in features could be characterized as a symplesiomorphy or synapomorphy varies in relation to different levels of the systematic hierarchy." (Ax 1987, 144) Symplesiomorphy and synapomorphy are terms referring to ancestral homology and derived homology respectively. Ax (1987, 144) goes on to discuss via his "three auditory ossicles" example how the "levels of the systematic hierarchy,"—the scope of the phylogenetic analysis—determine whether this character is an ancestral homologue or a derived homologue.

Recall that 'has three ear ossicles' is a derived homologue of mammals; nonmammalian tetrapods have a single ear ossicle as well as two jaw bones which are, collectively, homologous with the three ear ossicles of mammals. So when the scope of a phylogenetic analysis includes both mammalian and non-mammalian tetrapods, the character state 'three' of the 'number of ear ossicles' character is shared by all the mammals in the analysis as well as their most recent common ancestor; any nonmammalian tetrapods included in this phylogenetic analysis, will share the ancestral state, 'one,' for the 'number of ear ossicles' character. Ax (1987) points out the inadequacy of 'three ear ossicles' as a taxonomic character for the comparison of two placental mammals like humans and cats. In this case, the character state 'three' of the 'number of ear ossicles' character is shared by humans, cats, their most recent common ancestor, and other more distantly related ancestors; it is an ancestral homologue. Since ancestral homologues, unlike derived homologues, are shared by more distantly related ancestors as well, they do not distinguish the organisms under study from their ancestors and thus have no bearing on phylogenetic evaluations (Ax 1987, 146).

Since the scope of a phylogenetic evaluation determines which homologues are derived and which are ancestral, it determines the characters that are of interest to cladists and influences which individuation of those characters is satisfactory for a given phylogenetic analysis. When the scope of the phylogenetic analysis is narrowed to include only placental mammalian taxa, the individuation of characters for that phylogenetic analysis must be reconsidered. It may be the case that the three auditory bones would need to be individuated as separate elements in order for the branching order of humans and cats to be established. For instance, if each auditory bone has evolved differently in humans than it has in cats but the number of ear ossicles remains the same, it would not make sense to individuate the 'three ear ossicles' as a single character. No change at all would be quantified by such an individuation and the differences between human and cat ossicles would be ignored. So when the phylogenetic analysis includes mammals and non-mammalian tetrapods like lizards and amphibians, accounting for scope requires that we include 'three ear ossicles' as a single character rather than as multiple characters. When the scope of the phylogenetic analysis is restricted to placental mammals like humans and cats, however, it makes more sense to individuate the 'three ear ossicles' separately so that any changes within the ear ossicle complex are quantified. For these reasons, cladists need a principle of character individuation which can account for the scope of the phylogenetic analysis.

5.2.3 Taking Evolutionary Processes into Account

Returning once again to Richards' (2003, 287) suggestion that a principle of character individuation can only be satisfactory if it functions to support the goal of reconstructing "the branching order of the evolutionary past," we must take another aspect of context into account. If Richards' (2003) suggestion is correct and cladists are trying to reconstruct the branching order of the evolutionary past, surely the processes by which that evolution occurred should be taken into account when individuating characters. Winther's (2009) requirement that character abstraction be influenced by the 'real world' also speaks toward taking evolutionary processes into account. While Winther's (2009) causal grounding criterion is designed to ensure that causal process is taken into account for determining homology of characters, I suggest that causal grounding is also important for character individuation.

Let us take a closer look at the three middle-ear ossicles found in mammals, the *stapes*, *incus*, and *malleus*. These three little bones function together with the mammalian eardrum to transmit and amplify sound from a mammal's environment to its inner ear (Mallo 2001, 410). Given the variation in density from air to body tissue,

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without a relay system to capture and transmit sound waves from the air, mammals would not be able to hear anything because the sound waves would just reflect off their body tissue (Mallo 2001, 410). Mallo (2001) looks at the affects of gene mutation on the earossicle complex and finds that a variety of genes contribute to its formation. While a single gene mutation may only affect the development of one or two of the ear ossicles, the complex ceases to function in each case (Mallo 2001).

> Like other complex structures in the organism, the middle ear is more than the sum of individual components. These have to be connected in the proper fashion to be capable of functional activity. (Mallo 2001, 415)

The shape and position of each ear ossicle affects the function of the complex, and the development of the complex as a whole depends on the development of each ear ossicle individually. Taking these causal processes into account, the ear ossicles seem to be 'naturally' individuated as a functional complex as well as individual units within that complex.

The 'natural' individuation of the reptilian homologues of the mammalian ear, however, is a little different. While the *stapes* functions in sound transmission in the middle-ear of non-mammalian tetrapods as well, the mammalian *incus* and *malleus* are homologues of non-mammalian tetrapod jaw bones, the *quadrate* and *articular* (Meng et al. 2011, 181). The *quadrate* and *articular* make up the reptilian jaw joint, functioning together as a hinge in the feeding mechanism (Meng et al. 2011, 184). In this case, the 'natural' individuation seems to require that the *quadrate* and *articular* be individuated as a single, functional complex, contributing to a larger feeding complex. Under such an individuation, there are not one or three characters accounted for by the homologues of the mammalian ear bones, there are two—the '*stapes*' and the '*quadrate-articular*'.

Recent investigation into the development of the mammalian ear ossicles in marsupials shows the use of this *quadrate-articular* jaw joint for nursing when marsupial offspring are in their mothers' pouch (Takechi and Kuratani 2010, 421). At this stage of marsupial development, the mammalian jaw joint-dentary-squamosal joint-is not strong enough to support feeding and the quadrate-articular joint has not yet separated from the jaw to become two of the three mammalian ear ossicles (Luo 2007, 1016; Takechi and Kuratani 2010, 421). These marsupials have a functioning quadratearticular joint at one stage of development and then a functioning three-bone middle ear later on. As their mammalian jaw-joint strengthens, their quadrate and articular detach from it and move upward into the middle ear (where they are the incus and malleus respectively) (Luo 2007, 1016; Takechi and Kuratani 2010, 421). In this case, the 'natural' individuation seems to require, first, that the quadrate-articular joint be individuated as a single, functional complex that is part of a larger feeding complex and, second, that the *incus* and *malleus* be individuated as parts of the larger middle-ear complex.

With such a variety of different causal processes in the function and development of the same three bones in different organisms, there seem to be a variety of 'natural individuations' for the same characters. Multiple individuations of the same characters are not surprising if evolutionary processes like natural selection are taken into account as well. Organisms using these bones for feeding will be able to respond to a variety of different selection pressures than will organisms using the same bones for hearing.

5.2.4 A Context Sensitive Unequivocal Principle of Character Individuation

In summary, cladists need an '*unequivocal principle of character individuation*'—a principle which unambiguously specifies a single character individuation for each taxonomic input. Since the taxonomic input varies with the scope of the phylogenetic analysis, cladists need such a principle to take the scope of each phylogenetic evaluation into account. Moreover, a different 'natural individuation' may have occurred in the evolutionary past by different evolutionary mechanisms or aspects of evolutionary mechanisms. For this reason, it seems that evolutionary mechanisms and processes need to be taken into account by any satisfactory principle of character individuation. While scope of analysis and evolutionary mechanisms may not be the only aspects of context that a principle of character individuation needs to take into account, cladists seem to need an '*unequivocal principle of character individuation*' which is context sensitive, a principle which unambiguously determines the character set in each context.

5.3 A Place to Start

Winther's (2009) six objectivity criteria, introduced in section 4.1.6, take evolutionary processes into account with their in-depth scrutiny of proposed homologues. Since homologues are the same character in various instances—the heritable variation required for evolution by natural selection to occur—homologues are the characters 'individuated' by evolution. Winther's 'causal grounding' and 'inter-disciplinary communication' criteria allow for an investigation of the mechanisms at work in the development and evolution of each homologue. In our discussion of the various functions of the *stapes*, *incus-quadrate*, and *malleus-articular* homologues in different organisms, both evolutionary processes and developmental processes were taken into account. Evolution seems to have 'individuated' the middle-ear ossicles—*stapes*, *incus*, and *malleus*—together as a functional complex that ceases to function with minute developmental changes (Mallo 2001). The development of marsupial offspring involves a stage in which two of the middle-ear ossicles—*incus* and *malleus*—are used as their reptilian homologues—*quadrate* and *articular*—for feeding before they move into the middle-ear (Luo 2007, 1016; Takechi and Kuratani 2010, 421). Without this type of indepth investigation and testing, neither the homology nor the 'natural' individuations of characters could be determined.

As we discussed in section 4.4.3, however, Winther (2009) has a lack of concern for the character *individuation* problem such that his criteria alone do not provide any guidance for the individuation of characters. Any criteria or principle which hopes to solve the character individuation problem will include context sensitive rules for guiding the 'lumping' or 'splitting' of characters. I have discussed what sensitivity to scope and causal mechanisms might look like with respect to context sensitive character individuation, but more work needs to be done in order to complete the list. Only once we have determined what a satisfactory principle of character individuation requires can we determine whether or not such a principle is available to taxonomists.

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