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Phylogenetic Inference via Ancestral State Reconstruction/Character Mapping is Logically Unsound Abductive Reasoning

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Abstract

Ancestral state reconstruction (ASR) and the related method of character mapping (CM), have become increasingly popular, wherein it is claimed phenotypic characters are causally accounted for by fitting those characters on a phylogenetic tree previously inferred to explain sequence data. In this paper I show that in the scope of established deductive and non-deductive forms of reasoning applied in the process of scientific inquiry that ASR/CM are logically unsound methods leading to specious conclusions. The problem rests on the fact that inferences of phylogenetic, as well as all other classes of systematics hypotheses, à la taxa, are instances of abductive reasoning. Abductive inferences involve the conjunction of a theory of cause-effect relations to observed effects in order to conclude a plausible hypothesized cause or set of causes. As a matter of non-deductive reasoning, the requirement of total evidence (RTE) is relevant to abductive reasoning. ASR/CM fail as forms of abductive reasoning for two reasons: (1) violation of the RTE, and (2) the methods include as a premise a previously inferred phylogenetic tree that has no logical relevance to the present inference. The consequence is that ASR/CM leads to conclusions that cannot be interpreted as explanatory hypotheses.

Keywords: Evolutionary biology; abduction; deduction; induction; requirement of total evidence; systematics; taxonomy

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By denying scientific principles, one may maintain any paradox. — Galileo Galilei

1. Introduction

Much of the attention given to phylogenetic inference since the 1960's has centered on algorithmic approaches. Coupled with this emphasis, systematics has adopted a variety of ways to infer phylogenetic hypotheses [1–4], albeit consideration of what logical form of reasoning actually characterizes phylogenetic inference has been largely neglected. In the absence of acknowledging what class of reasoning specifically applies to phylogenetic inference, three contradictory approaches have become popular: (a) inferring hypotheses from all relevant characters, colloquially termed 'total evidence analysis,' though not to be confused with the philosophical requirement of total evidence [5–20]; (b) inferring separate sets of hypotheses from partitioned data, often sequence versus phenotypic characters, followed by comparing respective tree topologies as opposed to the hypotheses implied by those trees [19]; and (c) inferring hypotheses, most often explaining sequence data, then mapping, fitting, or 'optimizing' phenotypic characters onto those trees; what has commonly come to be known as 'ancestral state reconstruction' or ASR [21,22]. While ASR (sometimes referred to as ancestral state estimation) utilizes a stochastic approach [22], character mapping (CM) entails both ASR and the use of 'parsimony' as an optimization criterion for placing phenotypic characters onto a tree. For the purposes of this paper, ASR/CM will be used to denote the two approaches when appropriate. Topics (a) and (b) have been previously critiqued [18,19], and (c) was initially assessed [19] only in relation to character mapping via parsimony as violating the requirement of total evidence. A recurrent theme running through those discussions of (a)–(c) has been the importance of acknowledging what species of logical inference is being used when inferring phylogenetic hypotheses; indeed, a consideration that applies as well to inferences of all classes of hypotheses in systematics. Regardless of such concerns, ASR specifically has garnered widespread use. For instance, Wu et al. [23] (p. 2) state,

> "Ancestral state reconstructions (ASR) is an increasingly popular method to map morphological or ecological traits onto a molecular phylogeny [*sic*], which has provided plenty of novel evolutionary insights. With it, we can examine the character evolution of traits, reveal the homology of the characters of interest, study morphological conservatism and homoplasy, test for variation in rates of diversification, detect correlated transitions between two characters in evolution, explore how microevolutionary processes are linked to macroevolutionary patterns in evolutionary radiations, and re-evaluate past classifications."

Likewise, Revell [22] (p. 1, emphasis original) claims,

> "Ancestral state reconstruction falls within the domain of phylogenetic comparative methods… typically employed *downstream* of phylogenetic inference to test hypotheses about evolution based on a tree, and often in combination with trait data for the taxa of that tree…. Undertaking ancestral state reconstruction requires that we have a reconstructed tree…, as well as observations of a phenotypic trait of interest from some or all of the terminal taxa of that tree."

And a similar view is expressed by Cockx et al. [24] (pp. 3–4), using the phrase 'ancestral state estimation':

> "Testing hypotheses about the timing, sequence, and rate of integument evolution in early avians requires rationalization of the distribution of feather morphotypes within a phylogenetic framework…. To this end, statistical likelihood-based Ancestral State Estimation (ASE) methods have been applied. These methods utilize three components: a phylogenetic tree with branch lengths representing time or evolutionary rate; an evolutionary model describing the process by which a trait changes through time; and a set of observed character states corresponding to the tree tips (i.e., observed states in extant or fossil taxa)."

The key elements of ASR/CM are that sequence data are apparently regarded as having some intrinsic importance for inferring phylogenetic hypotheses not offered by phenotypic characters, e.g., [4,25], yet phenotypic characters are to be causally understood only after a phylogenetic tree is inferred from sequence data, or in paleontological cases fitting additional characters onto a previously inferred phylogenetic tree accounting for other phenotypic characters [26,27]. For instance, Griffith et al. [28] (p. 494) state,

> "Modern statistical methods [*sic*] of ancestral state reconstruction require three pieces of information: a phylogeny, character state data for taxa in the study (e.g., oviparity and viviparity), and a statistical model of evolution that incorporates parameters such as the rate of transition between character states. With this information, one can estimate the character state of hypothetical ancestors of the sampled taxa, quantify how often transitions

> between each state occur across the phylogeny, and calculate the relative rate at which they occur."

The reality is that ASR/CM offers results that should be treated as questionable in light of concern as to the form of reasoning that characterizes phylogenetic inference. In this paper I present a novel argument showing that ASR/CM is not a logically sound form of inference, precluding the opportunity to rationally explain occurrences of phenotypic characters. This argument complements and builds upon my earlier criticism [19] that phenotypic character mapping violates the requirement of total evidence.

In order to demonstrate the inadequacy of ASR/CM, it first will be necessary to identify the class of inference used in producing explanatory hypotheses in systematics, inclusive of phylogenetic hypotheses as implied by phylogenetic trees. This goes beyond the banal discourse of parsimony versus likelihood versus Bayesianism that has long consumed discussions in systematics (e.g., [1–4]. What is required from the start is acknowledging that the basis of scientific inquiry places constraints on hypothesis inference, followed by recognizing the operational relations between classes of reasoning, of which there are only three, in order to discuss the inferential nature of all taxa. These more general considerations will enable showing that ASR/CM is inconsistent with established norms for inferring explanatory hypotheses, thereby denying application of the method and any conclusions derived from it.

2. Root of the Problem: Filling the Inferential Void in Systematics

Subsequent to the introduction of cladistics 60+ years ago as the means to infer phylogenetic hypotheses, biological systematics has been consumed with the topic of how those hypotheses are to be inferred, at least from an algorithmic standpoint. Three perspectives have been prominent, often vying for superiority (Figure 1). From the 1960's to the present there has been the view that the principle of parsimony provides the appropriate framework, relying largely on the writings of philosopher of science Karl Popper, e.g., [29–33]. In the late 1970's an alternative opinion was introduced [2,34,35], wherein phylogenetic inference is presumed to be a statistical problem, with the suggestion that the likelihood principle [36–38] offers a more suitable means of inference. The emphasis on likelihood initially centered on inferences of phylogenetic hypotheses based on sequence data, with claims that the method allows for taking into consideration rates of sequence substitution, coupled with the argument that with ever-increasing inclusion of data, likelihood exhibits the quality of statistical consistency [1,2,34,39–41] (but see [42,43]), while sustained use of parsimony will lead one toward incorrect [*sic*] conclusions. Continuing the statistical mindset, it was suggested in the early 2000's that Bayesian reasoning is an appropriate method to infer phylogenetic hypotheses [44,45]. While advocacy for parsimony, likelihood, or Bayesianism, has varied in recent decades, it is not uncommon to find research publications reporting results using all three methods [46,47], or likelihood and Bayesianism, typically with comparisons being made between results with regard to phylogenetic tree topologies. Congruence between trees is assumed important, albeit inferential or scientific bases for such claims are nonexistent [19,48].

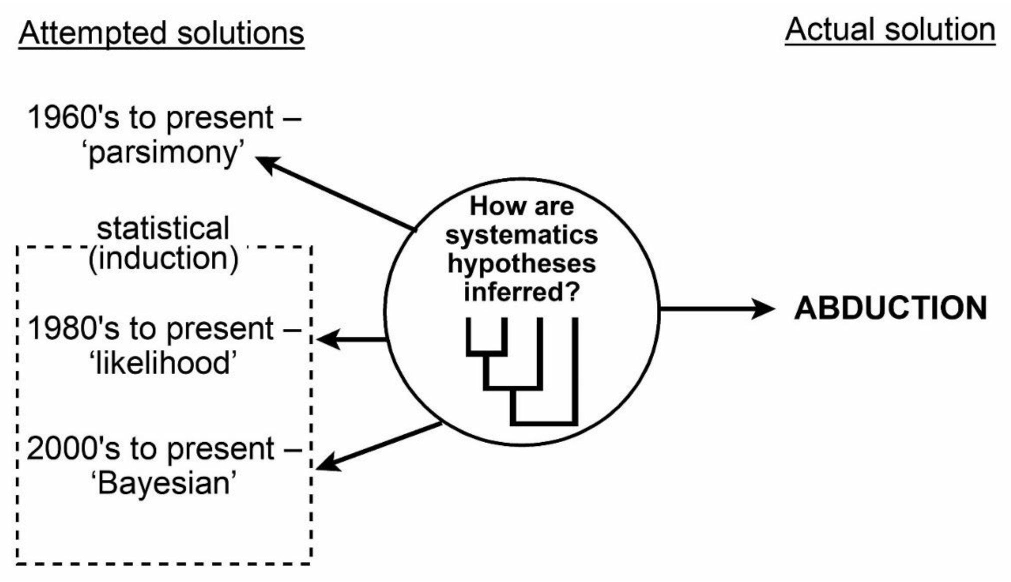

Figure 1. Answering the question of how systematics hypotheses, especially phylogenetic, are to be inferred has led to three attempted solutions versus the actual solution.

A conspicuous omission in most of the recent history of systematics has been the acknowledgement that neither parsimony, likelihood, nor Bayesianism are inferential forms capable of producing the explanatory hypotheses implied by phylogenetic trees [42,49,50]. This oversight is largely due to the fact that emphasis in systematics has been on algorithms, to the exclusion of recognizing the actual form of reasoning that characterizes inferences of hypotheses, whether explanatory or statistical. Parsimony is a criterion for selecting among *previously inferred* hypotheses; parsimony is not itself a class of reasoning capable of inferring hypotheses. Parsimony might be obliquely conceived as serving a role in algorithmic inferences of phylogenetic hypotheses [50], but only to the extent that the algorithm selects hypotheses on the basis of 'tree length' as a proxy for minimizing *ad hoc* hypotheses of homoplasy. This does not, however, establish parsimony as a form of inference. Minimizing tree length in algorithmic phylogenetic inference is merely a means to maximize explanatory hypotheses of homologous characters by way of common causes, colloquially, 'common ancestry.' Beyond that, phylogenetic hypotheses cannot be said to the products of inferences suitably called a 'parsimony method.'

In contrast, distinct from systematics, likelihood and Bayesianism have specific roles in the *testing* of hypotheses, not the *inferences* of hypotheses. Likelihood pertains to support for hypotheses via test evidence [36–38,51–53], while Bayesianism quantifies changes in belief in hypotheses subsequent to the introduction of test evidence [11,52,54]. Likelihood and Bayesianism are relevant *after* hypotheses have been inferred. While likelihood is commonly represented as $L(h \mid e) = P(e \mid h)$, the probability of test evidence e given the truth of hypothesis h highlights the view that predicted test evidence should have the lowest probability of occurrence unless the causal conditions stated by the hypothesis occurred. This is equivalent to Popper's 'severity of test' criterion [29,55–60]. As characterized by Royall [53, see also 51]),

> "This [law of likelihood] says simply that if an event [= test evidence] is more probable under hypothesis *A* than hypothesis *B*, then the occurrence of that event is evidence supporting *A* over *B* — the hypothesis that did the better job of predicting the event is better supported by its occurrence. It further states that the *degree* to which occurrence of the event supports *A* over *B* (the strength of the evidence) is quantified by the ratio of the two probabilities."

Likelihood expresses support for *h* given the actual available test evidence *e*. It is not uncommon to find confusion on this matter in the systematics literature. For instance, regarding phylogenetic hypotheses, Harmon [61] (p. 24) (see also [1,22,62]) states, "In an ML framework, we suppose that the hypothesis that has the best fit to the data is the one that has the highest probability of having generated that [*sic*] data." Of course, the data referred to are the characters used to infer the hypothesis in the first place, given that our aim is to explain those characters. Those data are not test evidence as intended by the likelihood principle. Interpreting organismal characters as evidence in $P(e \mid h)$ is to misinterpret likelihood. The probability of one's observation statements regarding organismal characters are not relevant to likelihood, as those statements occur prior to hypotheses even being inferred. Assuming one trusts their observation statements, which is a prerequisite in the first place for inferring hypotheses causally accounting for those effects, the probability of observations, as a matter of belief, would be unity. Of course, this prerequisite is often violated in phylogenetic inferences using so-called 'likelihood' or 'Bayesianism' [50] (cf. *3.2. Why-Questions*). The 'highest probability of having generated those data' under the likelihood principle refers to the anticipation of observing test evidence *e* given *the truth of the hypothesis* and *once that evidence has been subsequently found during the process of testing*.

Similar to the misunderstanding of likelihood in relation to hypothesis inference, a similar problem exists for Bayesian inferences of phylogenetic hypotheses. While Bayes' Theorem is given as,

$P(h \mid e) = P(h) \cdot P(e \mid h) / P(e)$,

evidence *e* once again refers to test evidence, such that $P(h)$ is probability the hypothesis is true prior to the introduction of test evidence. $P(e \mid h)$ is probability of finding predicted test evidence if the hypothesis is true, and $P(e)$ is the probability of finding the test evidence regardless of the hypothesis. Bayesianism quantifies changes in hypothesis belief contingent on the introduction of new test evidence. In other words, the change from prior probability, $P(h)$, before testing, and posterior probability, $P(h \mid e)$, given the result of testing. The supposed interpretation of Bayes' Theorem that is claimed applicable for inferring phylogenetic hypotheses is,

$P(tree \mid data) = P(tree) \cdot P(data \mid tree) / P(data)$,

where *data* refers to organismal characters in need of being explained, not test evidence, and the *tree* refers to a branching diagram, not the actual set of hypotheses implied by that diagram subsequent to the inference [44,45]. The rendition used in systematics is not Bayesian in that it misconstrues both the intent and content of the theorem. More importantly, it is not possible to interpret Bayes' Theorem as testing phylogenetic trees via homologous characters, much less infer phylogenetic hypotheses in any explanatory context [42,48]. To be clear, a phylogenetic tree *qua* branching diagram is not a phylogenetic hypothesis; it is a diagram that only attains utility if it implies several distinct classes of explanatory hypotheses [43,63,64] (cf. *3.6. Inferences of Phylogenetic Hypotheses*). A phylogenetic hypothesis is therefore a composite construct intentionally conveyed by a phylogenetic tree. What should be inferred are phylogenetic hypotheses, not phylogenetic trees.

In the scope of formal logic and the objective of scientific inquiry (cf. **3. Systematics as Scientific Inquiry**), likelihood and Bayesianism are forms of inductive reasoning *sensu stricto*, i.e., the testing of hypotheses. Likewise, parsimony has been associated with testing, such as Popper's [29] view that parsimonious hypotheses are more open to being tested compared to less simple alternatives [30], and this presumes hypotheses were previously inferred. The view that phylogenetic inference is a statistical issue, warranting application of likelihood or Bayesianism, seems to have arisen as a consequence of confusing the inferences of hypotheses with their being tested. If one's understanding of logic is limited to only deductive and inductive reasoning, e.g., [65,66], then it might be assumed reasonable to think statistical inference appropriate to the problem of inferring phylogenetic hypotheses, but this is mistaken. The problem is that statistical methods are intended to test, not infer *statistical* hypotheses. The upshot is that whether systematists embrace parsimony, likelihood, or Bayesianism, each was introduced into systematics in an attempt to fill the role as reasoning that could allow for inferring phylogenetic hypotheses. Contrary to these attempts, there is only one form of reasoning that enables inferences of theories and hypotheses, which will be briefly mentioned next, then presented in greater depth later (cf. **3. Systematics as Scientific Inquiry**).

Given the assertion that phylogenetic hypotheses cannot be inferred via parsimony, likelihood, or Bayesianism, what class of reasoning enables such inferences? The extensive work of the philosopher of science Charles Sanders Peirce (1839–1914) during the second half of the 19th and early 20th centuries led to recognizing that the form of non-deductive reasoning that produces theories and hypotheses is abductive inference, or abduction [30, 67–75; see also 52, 65, 76–97]:

> "Abduction… is merely preparatory. It is the first step of scientific reasoning, as induction is the concluding step… Abduction makes its start from the facts, without, at the outset, having any particular [hypothesis] in view, though it is motivated by the feeling that a [hypothesis] is needed to explain the surprising facts. Induction makes its start from a hypothesis which seems to recommend itself, without at the outset having any particular facts in view, though it feels the need of facts to support the [hypothesis]. Abduction seeks a [hypothesis]. Induction seeks for facts" [69] (p. 2.106).

Together with deduction and induction, abduction was first described by Aristotle in his *Prior Analytics* [98,99], subsequent to which abduction was ignored for over 2000 years until Peirce's [67,100] work on operational relations between deductive and non-deductive reasoning in the service of scientific inquiry. Peirce emphasized that characterizing the process of scientific inquiry cannot be limited to deductive and inductive operations. He recognized that relations between deductive and non-deductive reasoning calls for distinct operational demarcations relative to the process of inquiry: *abduction*, inferences of hypotheses and theories, inclusive of statistical hypotheses and enumerative 'induction' [101–104]; *deduction*, inferences of predictions of potential test evidence; and *induction*, testing of hypotheses and theories. Peirce [68] (p. 5.171, emphasis original) summarized the situation this way,

> "Abduction is the process of forming an explanatory hypothesis. It is the only logical operation which introduces any new idea; for induction does nothing but determine a value, and deduction merely evolves the necessary consequences of a pure hypothesis.
>
> Deduction proves that something *must* be; Induction shows that something *actually is* operative; Abduction merely suggests that something *may be*.
>
> Its only justification is that from its suggestion deduction can draw a prediction which can be tested by induction, and that, if we are ever to learn anything or to understand phenomena at all, it must be by abduction that this is to be brought about."

This distinction between abduction and induction *sensu stricto* clarifies the roles of likelihood and Bayesianism as inductive, not abductive. Subsequent to Peirce's death, however, abduction was intentionally marginalized [105–107] or ignored [6,29,108] in philosophy of science during the first half of the 20th century. Inferences of theories and hypotheses were relegated to matters of psychology, with claims of lacking any logical form. Beginning with Hanson's [76] acknowledgement of the importance of abduction, there has been increasing recognition of abduction in fields such as science, law, artificial intelligence, as well as everyday living [87], not to mention relevance of the operational progression, abduction → deduction → induction, representative of much of scientific inquiry.

Characterizing phylogenetic inference as abductive was first given brief mention in the late 20th century [109–111], but concerted efforts to more fully examine the implications of abduction for systematics began in earnest in the mid-2000's [18,49,112,113], albeit acceptance of this reasoning in the broader systematics literature has been almost non-existent. The implication of acknowledging that phylogenetic inference is abductive is that it enables more formally and accurately representing the premises required to reach conclusions in the form of phylogenetic as well as other classes of systematics hypotheses [42,63,113–118]. Two significant, interrelated consequences ensue from specifying those premises. Brief mention will be given here and more extensively addressed later (cf. **4. The Case Against ASR/CM**): the first consequence pertains to the requirement of total evidence (RTE), which is a maxim of all non-deductive reasoning, making it irrational to engage in inferences for partitioned sets of characters or subsequent attempts to draw comparisons between tree topologies of separately inferred phylogenetic hypotheses; the second consequence is denial of the activity of ASR/CM.

The RTE was first formally recognized by Carnap [5, 6; see also 7–20], stating that one's belief or confidence in a hypothesis should be based on the total relevant evidence supporting that hypothesis, where the notion of support transcends all forms of reasoning in that it refers to the premises of an inference that serve as evidence for, or warrant a given conclusion [12]. Carnap [6] (p. 211) describes the RTE as follows: "…in the application of inductive logic to a given knowledge situation, the total evidence available must be taken as a basis for determining the degree of confirmation." Relevance is determined by evidence having a positive or negative influence on the credence of a hypothesis. The RTE has primarily focused on consideration of all relevant *test* evidence when determining support for theories and hypotheses. In other words, literature on the RTE almost uniformly pertains to inductive reasoning. While the requirement is automatically satisfied in deduction, given the rules for valid deduction, application of the RTE in non-deductive reasoning excluded specific consideration of abductive reasoning. This was largely due to the influence of logical empiricism during the first half of the 20th century, especially among such influential philosophers as Reichenbach [105–107], Carnap [6], Popper [29], and Hempel [7–10,108]. I [18,19] have noted that the RTE cannot be limited to induction, but should be more broadly construed as inclusive of the premises that pertain to abductive reasoning, at least in the case of systematics (cf. *4.1. Update on the RTE as a Critique of ASR/CM*).

While importance of the RTE for phylogenetic inference was first documented by Kluge [122] and discussed at length in the 1990's, e.g., [119–121], justification of the requirement relative to abductive reasoning in systematics was not recognized [18]. As discussed later (cf. **4. The Case Against ASR/CM**), Kluge's [122] association of the RTE with phylogenetic inference was based on incorrectly attempting to apply the RTE in the sense of treating homologous characters as test evidence for phylogenetic hypotheses.

With regard to ASR/CM, it might be argued that this approach does not violate the RTE, given that phenotypic characters are at least indirectly taken into consideration with sequence data. This is an erroneous supposition. I will show later that ASR/CM neglects to acknowledge the premises required to abductively infer phylogenetic hypotheses, such that ASR/CM is neither a logically recognized nor scientifically acceptable form of reasoning from a set of premises to a conclusion of explanatory hypotheses. The chief problem lies in the treatment of a phylogenetic tree as nothing more than a branching diagram serving as a premise in conjunction with premises comprising homologous phenotypic characters and a phylogenetic theory. It is not possible for this combination of premises to conclude phylogenetic hypotheses that can be interpreted as causally accounting for phenotypic characters mapped onto trees. Thus, the RTE is not satisfied because all relevant premises are not included in the inference, namely all relevant characters to be explained.

Recognizing the form of abductive reasoning required for phylogenetic inferences will make it apparent that ASR/CM is a scientifically baseless approach, leading to hypotheses that are uniformly unfounded. But first, the foundations of scientific inquiry will lay the groundwork for pursuing causal understanding via the operational relations between the different classes of reasoning, discussed next.

3. Systematics as Scientific Inquiry

Critiquing ASR/CM requires consideration of three interrelated topics often acknowledged as fundamental to scientific inquiry. These subjects will be discussed in three respective subsections: *3.1.*

Objective of Scientific Inquiry will identify that the pursuit of causal understanding is a consistent goal in all the sciences; *3.2. Why-Questions* will point out that observations of phenomena are linked to inquiry through implicit or explicit questions that seek answers in the form of explanatory hypotheses presenting past causal conditions accounting for observed effects. Answers to why-questions are products of abductive reasoning, which will be considered in *3.3. Forms of Reasoning*. Since abduction has only recently been recognized in systematics, brief attention will be given to distinguishing logical and operational differences between abduction, deduction, and induction, which lays the groundwork for critiquing ASR/CM.

3.1. Objective of Scientific Inquiry

There is general agreement that the goal of scientific inquiry is not only to describe phenomena, whether objects or events, but also the pursuit of causal understanding of what we encounter [8,13,56,76,123–138]. As noted by Ross [138] (p. 8), "Explanations provide deep understanding in a way that is distinct from other scientific projects such as mere description, prediction, and classification." In the context of systematics, both as a field of science and subfield of evolutionary biology, inquiry would proceed from describing the observed characteristics of organisms and subsequently inferring plausible past causal events that account for those observations as effects. Causal considerations in systematics typically span proximate and ultimate causes *sensu* Mayr [42,118,139,140], which is consistent with the perspective expressed by Uller and Laland [141] (p. 1), "Scientific inference typically relies on establishing causation. This is also the case in evolutionary biology, a discipline charged with providing historical accounts of the properties of living things, as well as an understanding of the processes that explain the origin of those properties."

3.2. Why-Questions

Science as a process of inquiry implies that it is routine to ask what-, how-, and why-questions, depending on the direction taken in inquiry. For the purposes of systematics and evolutionary biology, it is why-questions that are predominant, although what- and how-questions can eventually lead to the pursuit of hypothesized causes via why-questions.

Acknowledging the form why-questions take has several implications for the treatment of characters of organisms in relation to inferring explanatory hypotheses. Rather than having the form, 'Why is *q* the case?', why-questions should be contrastive, i.e., 'Why is *q* the case *in contrast to p*?' [13,14,18,43,49,125,142–145]. Ross [138] (pp. 6–7, emphasis original) highlights importance of the contrastive nature of why-questions:

> "Providing an explanation requires precisely specifying the explanatory target [i.e., the effect(s) to be explained]. This precision involves identifying the contrastive focus of interest and meaning of terms in the why-question. Consider the explanatory why-question: "Why does guinea pig A have spotted-coloring on its trunk?" Without further clarification, this question is ambiguous and does not sufficiently specify the explanatory target. For example, this question might be asking why guinea pig A has *spotted*-coloring on its trunk versus *solid* coloring; or why guinea pig A has spotted-coloring on its *trunk* as opposed to its *legs*; or why *guinea pig A* has this spotted-coloring as opposed to *guinea pig B*. Each of these contrasts refers to a different explanatory why-question that may have different answers. Specifying the explanatory target with precision is essential for ensuring that scientists are discussing the same explanatory question and not talking past each other. Clarity here helps avoid situations in which scientists mistakenly compare explanations without realizing that the explanations have different targets of interest and, thus, aim to explain different things. This is especially important because natural phenomena can be represented in different ways and have distinct features, which emphasize different contrasts that we might want to explain."

For any why-question, 'Why is *q* the case *in contrast to p*?', the contrastive form treats observation statement *q* as the *fact* to be explained, and *p* as the *foil*, a condition ordinarily expected or previously explained. The nature of the contrast is what warrants the question: a surprising or unexpected *fact* is in need of explanation *in contrast to* what is normally expected. The fact/foil distinction is present in data matrices used to infer phylogenetic hypotheses, when outgroup (= *foil*) and ingroup (= *fact*) organisms (not taxa) and associated characters are indicated, such that each column in the matrix implies a contrastive why-question [43,63,144]. The contrastive form of why-questions ensures that explaining a fact entails also explaining the foil, and while those explanations are effects of separate causal events, they should be due to the same class of cause [142,146]; see also [147–155]. Designations of outgroups and ingroups accommodate this requirement [144].

An additional condition of why-questions is that there is the presupposition that fact and foil are true observation statements [142,146,156–159]. Regarding systematics, this would entail that observation statements of homologous characters are presumed true. Without this presupposition there would be no basis for asking why-questions in the first place since one would have to admit that they cannot trust statements of similarity. I [43,50] have previously discussed implications of this presupposition in relation to sequence data being explained by taking into account evolutionary rates by using so-called likelihood and Bayesian methods. Invoking rates implicitly assumes one does not trust their observation statements of homologous characters, which warrants not explaining characters via common causes. The consequence is this allows for an excess of *ad hoc* hypotheses of homoplasy, which again is contradictory to the presupposition that observation statements are true. As will be noted later (cf. *3.6. Inferences of Phylogenetic Hypotheses*), correcting this problem entails renaming relevant initial homologous characters as different prior to inferring phylogenetic hypotheses, assuming an empirical basis for renaming can be provided.

3.3. Forms of Reasoning

If the goal of scientific inquiry is to acquire causal understanding, and why-questions are the conceptual link between observations and the attainment of understanding, then the established forms of reasoning are what enable inferences to answers in the form of explanatory hypotheses and subsequent procedures for empirical evaluations of those hypotheses. Presenting forms of reasoning has traditionally been the purview of formal logic, and often limited to only recognizing deduction and induction, e.g., [11,12,160,161]. I noted earlier (cf. **2. Root of the Problem: Filling the Inferential Void in Systematics**) that especially since the latter half of the 19th century, the operational aspects of reasoning for the purpose of inquiry require a finer distinction; deduction, plus two forms of non-deductive reasoning: induction *sensu stricto* and abduction [65,67–75]; see also [30,52,76,78–88,90,92–96,162]. Even in recent treatments of logic, however, abduction is still commonly overlooked or subsumed under induction, e.g., [66,163,164] For purposes of characterizing scientific inquiry, including systematics, it is more accurate to regard abduction as distinct from induction. Each form of reasoning plays a role in the stages of inquiry: abduction involving inferences of theories and hypotheses, predictions of potential test evidence are deductively obtained, and subsequent testing occurs via induction. Operational relations between ab-, de-, and induction received extensive attention in the late 19th and early 20th centuries by Charles Sanders Peirce [67–75], but full appreciation of Peirce's ideas did not become realised until the second half of the 20th century [30,76,78,79,82,84–88,90,92–96].

Relative to systematics, relations between the three stages of inquiry have been discussed by me [18,42,48,49,60,63,112,116,118,165], Mortimer et al. [64], and Martínez-Bautista [162]. Of immediate significance is abduction, given that inferences of explanatory hypotheses as means of causally accounting for homologous characters observed among organisms is the most common operation [18,19,42,43,48–50,60,63,112–118,165]. Contrary to popular belief since the advent of cladistics, testing the variety of classes of hypotheses in systematics, especially specific and phylogenetic, rarely, if ever, occurs [48,118,165]. The emphasis on support typical in recent systematics research should not be

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confused with support via test evidence, where the former is due to incorrect application of the bootstrap or uninterpretable values offered by the Bremer index [42,48].

Examples of each stage of inquiry, with emphasis on systematics, can be represented by the following arguments. Double or single lines, separating premises (above) and conclusions (below) indicate non-deductive and deductive arguments, respectively:

§1 **Abduction, inferring hypotheses as answers to why-questions:**

- background knowledge *b*, e.g., assumption that observation statements are true
- theory(ies) *t*, e.g., 'common ancestry'
- observed effects, as differentially shared, homologous characters
- explanatory hypotheses, *h*, implied by cladograms or phylogenetic trees

§2 **Deduction, predictions of consequences given the truth of hypotheses:**

- background knowledge *b*
- theory(ies) *t*, relevant to observed effects in **§1**
- specific causal conditions presented in explanatory hypotheses *h* via **§1**
- proposed conditions needed to perform test(s)
- observed effects, as differentially shared characters, originally prompting *h* (cf. **§1**)
- predicted test evidence, i.e., effects associated as closely as possible with specific causal conditions presented in hypotheses

§3 **Induction, hypothesis testing:**

- background knowledge *b*
- theory(ies) *t*, relevant to observed effects in **§1**
- test conditions performed/observed
- confirming/disconfirming evidence [observations of predicted test evidence in **§2**, or alternative observations]
- *h* is confirmed/disconfirmed.

Regarding forms of reasoning in **§1–§3**, deduction is non-ampliative, meaning conclusions do not introduce facts beyond what are already offered in the premises. Non-deductive reasoning is, in contrast, ampliative; the content of conclusions extends beyond what are provided in the premises. This enables abduction to introduce new ideas, such as plausible hypotheses of unique past causal conditions, whereas inductive conclusions suggest that tested hypotheses are operative for future consideration. While there is the assumption that premises are true for all forms of reasoning, only deductive conclusions are necessarily true, hence deduction is sometimes referred to as necessary or ideal reasoning. Being nonampliative, neither abductive nor inductive reasoning guarantee true conclusions. Abductive conclusions are deemed plausible, in the sense that Peirce [75] (p. 8.223) suggested: "By plausibility, I mean the degree to which a theory [or hypothesis] ought to recommend itself to our belief independently of any kind of [test] evidence other than our instinct urging us to regard it favorably." While abduction leads to plausible hypotheses, consideration of probability pertains to observed effects being explained [166] (p. 139): "…the conclusion of an abductive argument is plausible if the minor premise [observed effects, organismal characters; cf. **§1**] is highly probable given the major premise [theory, e.g., 'common ancestry'] and the conclusion [hypothesis]. This is an indication of how probability plays a role in abduction". In contrast to abduction, probability in induction pertains to conclusions, given the test evidence present in premises that provide the basis for the hypothesis receiving positive test support or confirmation (cf. **§3**), with induction sometimes referred to as probable reasoning. It is worth reiterating that Bayesianism is inductive, which immediately precludes it from inferring phylogenetic hypotheses in lieu of abduction. This general sentiment is expressed by Gómez and Fontaine [167] (p. 482),

> "Such a Peircean understanding of abduction precludes from the very start of this work a Bayesian approach, in which hypotheses would be introduced on the basis of degrees of credence, or probability, or any other statistic support. Indeed, probability is concerned with induction. And… there cannot be induction without previous abduction by

> means of which is introduced the hypothesis to be tested. Therefore, it must be clear since the beginning that abduction is neither deduction nor induction, nor even a mix of both."

Recall that contrastive why-questions entail the presupposition that observation statements are true, expressed in the background knowledge in **§1** and the third premise, observed effects/homologous characters. The consequence is that a common-cause theory [11,13,33,168–171] would be applied to those effects such that explanatory hypotheses maintain as much as possible the integrity of true observation statements.

The example of abduction in **§1** is the simplest representation of phylogenetic inference. Abduction to the two most common classes of explanatory hypotheses in systematics, specific (species) and phylogenetic inferences, will be considered next.

3.4. Abductive Reasoning and the Nature of Taxa

Pursuant to the topics presented in the previous section, it follows that in the context of evolutionary biology, inclusive of systematics, the phenomena we most often describe are organisms by way of the properties they instantiate. From these properties we abductively infer explanatory hypotheses as part of the process of attaining causal understanding. A consequence is that consideration of taxa should not be either as class constructs, groupings or collections of things, or concrete entities, but rather as the variety of explanatory hypotheses routinely inferred as part of inquiry. A point that will be made apparent in the next two subsections, *3.5. Inferences of Specific (Species) Hypotheses* and *3.6. Inferences of Phylogenetic Hypotheses*, is that both classes of hypotheses are composite constructs, in that they imply a multitude of past causal events that account for properties of organisms.

Equating taxa with explanatory hypotheses serves to acknowledge that taxa are abductively-derived answers to implicit or explicit why-questions. These answers include specific (species) and phylogenetic hypotheses, although additional classes of explanatory hypotheses should be regarded as taxa. Figure 2, modified from Hennig's [172] figure 6; (cf. [42,49,63,113–115,117,118]), presents common classes of hypotheses in systematics. Hennig [172] (p. 31) referred to this figure as "The total structure of hologenetic relationships," clearly indicating *causal* relationships. Figure 2H inclusive denotes a vertical time axis, with individuals in the present situated along the top and lines connecting individuals representing past tokogenetic events. Ontogenetic relationships (Figure 2B) indicate causal events during the life of an individual. Relationships referred to in the figure are clearly causal constructs, such that the diagram implies past, albeit quite vague, causal events in the form of novel character origin and fixation among individuals in populations (Figure 2F, G, H), as well as a causally unspecified population splitting event (Figure 2H).

While Figure 2C, E−H present what might be called 'lineages,' this term offers imprecise reference to past causal events that conceivably account for some of the characters of organisms observed in the present. The limited utility of lineages as hypotheses has implications for the popular view of species-as-lineages, e.g., de Queiroz's [173,174] 'general lineage concept' and 'unified concept of species' [175,176], or that a species is "the hypothesis that a group of populations represents a separately evolving and divergent lineage" [177] (p. 12). Reducing species to lineages only presents hypotheses of spatio-temporally restricted sets of past tokogenetic events. A common consequence is that species are incorrectly regarded as concrete entities, e.g., [176], not explanatory hypotheses referring to past spatiotemporally restricted tokogeny associated with novel character origins and fixation events that are intentionally inferred. Our interest is to causally account for the properties of organisms and some of those characteristics form the basis for inferring specific hypotheses. The characters of organisms are not just criteria for designating or 'delimiting' lineages; a lineage is part of the more inclusive composite hypothesis explaining particular organismal characters. Supplemental to the topic of lineages, it will be noted in the next subsection [*3.5. Inferences of Specific (Species) Hypotheses*] that characterizing abductive inferences of specific hypotheses moves us away from a focus on species 'concepts' to emphasizing the need for formal species theories that allow for different classes of hypotheses, albeit under the one term species, cf. [63,116]. This is not to imply that we should take a pluralist view of species, but rather to emphasize that the one term species is operationally inadequate for representing what in reality are multiple classes of hypotheses.

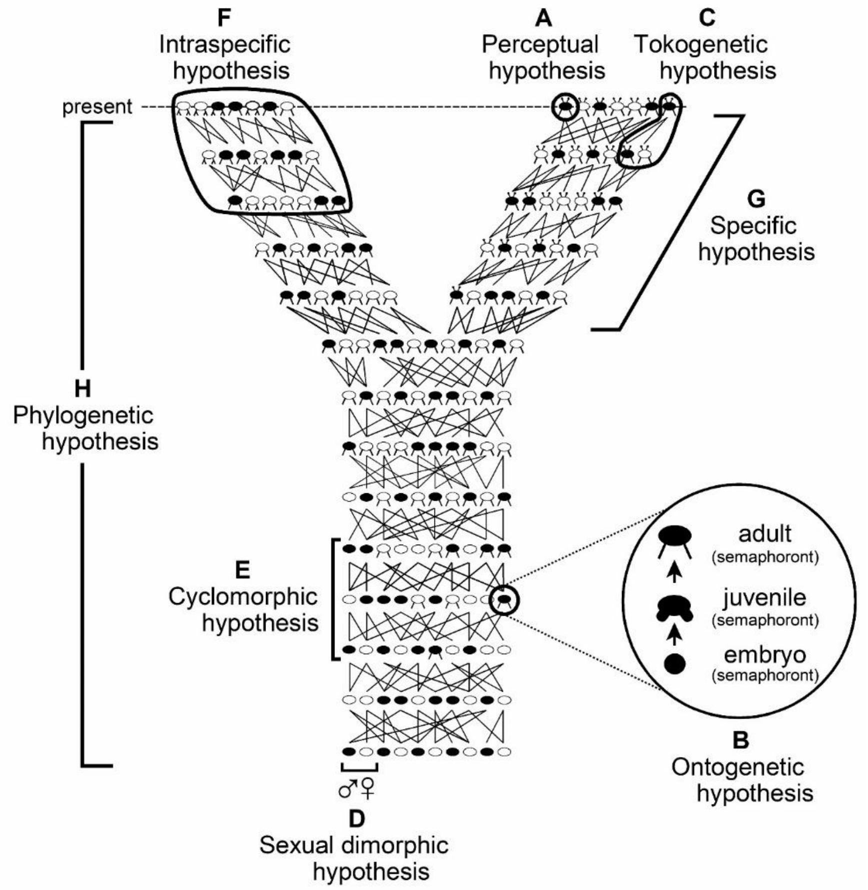

Figure 2. Some of the classes of hypotheses in systematics, based on Hennig (1966: figure. 6). Relations between eight classes (**A–H**) of explanatory hypotheses commonly inferred in biological systematics. Adapted from [43,63,64,116].

As explanatory hypotheses, taxa are neither described, discovered, nor delimited; all popular jargons incorrectly implying taxa are concrete entities, e.g., [178]. Individual organisms, what Hennig [172] termed semaphoronts (Figure 2B), are observed and described at specific moments in their life history [42,63,118], see also [114–117]; operational examples include [179–184]. Invoking causal relationships among semaphoronts is consistent with the objective of scientific inquiry and by extension evolutionary biology.

3.5. Inferences of Specific (Species) Hypotheses

Referring to inferences of species (Figure 2G) as explanatory hypotheses [63,113,115–117], the one term species cannot effectively represent the variety of hypotheses that transcend all organisms. Different causal processes can be considered in the fixation of novel characters among (a) gonochoristic or cross-fertilizing hermaphroditic individuals, as opposed to obligate (b) asexual, (c) parthenogenetic, or (d) self-fertilizing organisms, as well as (e) instances of horizontal gene transfer [116]. Ideally, the classes of explanatory hypotheses (a)–(e) should not be subsumed under the one term species, but should be clearly segregated to indicate the distinct explanatory nature of each.

A contrived example of inferring a specific hypothesis will illustrate the route from observations of semaphoronts to contrastive why-questions, inferences to hypotheses, and formal definition of a species name (Figure 3). This example is limited to composite hypotheses for gonochoristic or cross-fertilizing hermaphroditic organisms, referred to above, but with relevant modifications can be applied to the other classes of novel character fixation. In this example, there are new observations of individuals with dorsal antennae and ventral appendages (Figure 3A), prompting the contrastive why-question,

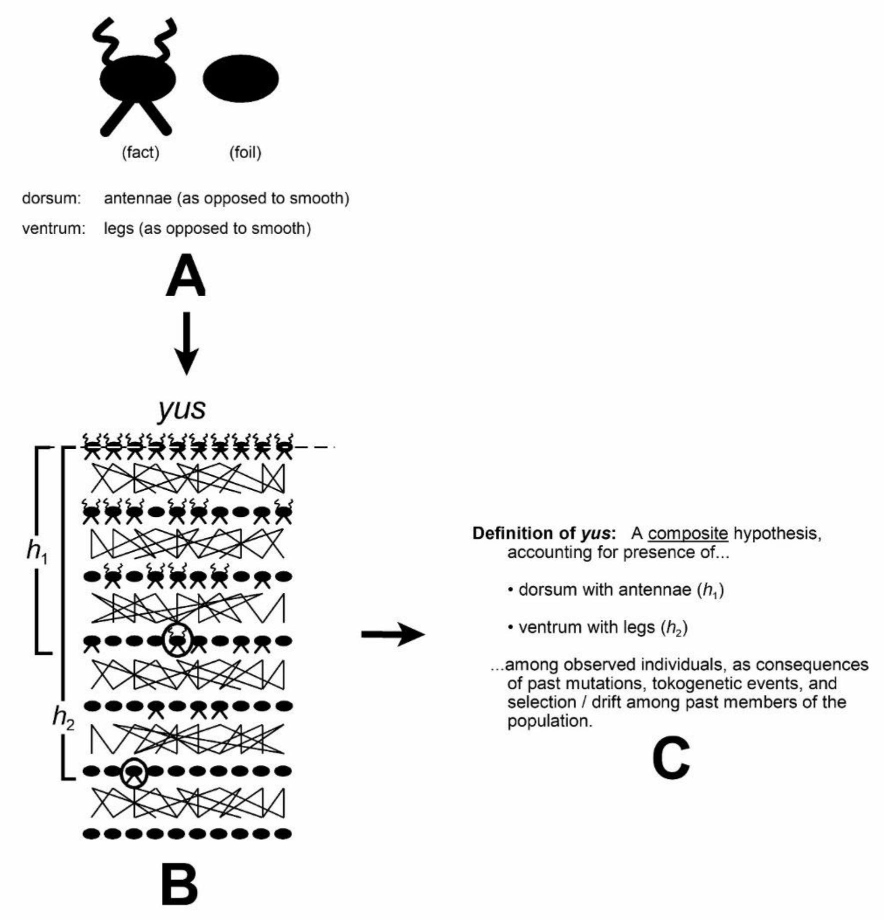

Figure 3. A specific, i.e., species hypothesis if often a composite construct causally accounting for two or more characters. (**A**) Presence of dorsal antennae and ventral legs are in need of being explained. (**B**) Specific hypotheses can be illustrated as lineages indicating spatiotemporally restricted events of novel character origin and fixation. (**C**) The definition of a formal species name refers to the explanatory hypothesis(es) causally accounting for particular characters. Modified from [63].

§4 Why do these individuals have dorsal antennae and ventral appendages (= facts) in contrast to convex dorsal and ventral margins (= foils) as seen among individuals to which specific hypothesis *xus* refers?

Notice that the formal name *xus* applied to this hypothesis is shown as a uninomial to underscore that specific and phylogenetic hypotheses are separately inferred [114,115,117,179]. The International Codes of Nomenclature, e.g., International Commission on Zoological Nomenclature [274], only recognize specific hypotheses when associated with phylogenetic hypotheses at the rank of genus, e.g., *Yus yus*, which does not acknowledge the independent inferences of the two classes of hypotheses. Answering the question in **§4** leads to the abductive inference:

§5 • *Background knowledge b*, e.g., assumption that observation statements are true

• Gonochoristic or cross-fertilizing hermaphroditic species theory:

If character $x(1)$ originates by mechanisms a, b, $c \ldots n$, among gonochoristic or cross-fertilizing hermaphroditic individuals of a reproductively isolated population with character $x(0)$, and $x(1)$ subsequently becomes fixed throughout the population during tokogeny by mechanisms d, e, $f \ldots n$, then individuals observed in the present will exhibit character $x(1)$.

- *Observations (effects):*

Individuals have dorsal antennae and ventral appendages in contrast to convex dorsal and ventral margins, respectively, as seen among individuals to which specific hypothesis *xus* refers.

- *Causal conditions (composite specific hypothesis yus; Figure 3B, C):*

Hypothesis h_1 – Dorsal margins as antennae originated by unspecified mechanisms within a reproductively isolated population with convex margins and eventually became fixed throughout the population during tokogeny by additional unspecified mechanisms;

Hypothesis h_2 – Ventral margins as appendages originated by unspecified mechanisms within a reproductively isolated population with convex margins and eventually became fixed throughout the population during tokogeny by additional unspecified mechanisms.

The character notation $x(1)$ denotes an observation statement in subject x – predicate (n) form, rather than the standard 'character – state' distinction. Objects are perceived by way of the characters *simpliciter* they instantiate, and are communicated through statements using subject-predicate relations [144]. For instance, 'The dorsal margin [subject] of this individual has antennae [predicate].'

Notice that the *Species theory* in **§5** differs from the standard 'species concept' approach in that the former specifies cause-effect relations regarding properties of organisms as opposed to the more acausal or limited causal forms typical of various species concepts. The emphasis on a species *theory* as opposed to a *concept* is on par with the goal of scientific inquiry, discussed earlier. Specific hypothesis *yus* in **§5** refers to a lineage (Figure 3B) insofar as it considers a reproductively isolated population over some span of time, implying the totality of past, spatio-temporally constrained tokogenetic events relevant to explaining the presence of antennae (hypothesis h_1) and ventral appendages (hypothesis h_2) (Figure 3B, C). Neither the *Species theory* nor composite hypothesis *yus* is the same as limiting species to being lineages, which lacks the overt explanatory intent explicitly intended by the *Species theory*.

The inference in **§5** leads to two distinct hypotheses. There is the assumption that the observed characters are independent with regard to events of character origin and subsequent fixation, but these hypotheses are subsumed under the more general causal condition that tokogeny is spatio-temporally constrained. This acknowledges that specific hypothesis *yus* is composite in form: $h_1 + h_2$ + spatio-temporally limited tokogeny. The reference to tokogeny then makes the characters being explained relevant to each other at the level of the population through time, meaning the requirement of total evidence applies to specific inferences, just as it does for phylogenetic inferences.

Given the why-question in **§4** and premises in **§5**, specific hypotheses are necessarily inferred separate from phylogenetic hypotheses. The reason is that the respective sets of why-questions and ensuing specific and phylogenetic premises are different. This is apparent when we next consider inferences of phylogenetic hypotheses.

3.6. Inferences of Phylogenetic Hypotheses

The depiction of abduction in **§1** is a simplified version of phylogenetic inference, with minimum premises leading to a conclusion of explanatory hypotheses implied by a phylogenetic tree or cladogram. A more comprehensive example is presented here, from which contrasts with inferences of specific hypotheses, cf. **§5**, can be shown.

Similar to inferring the composite specific hypothesis in **§5**, the basis for phylogenetic inferences would be to answer a contrastive why-question(s) [42,43,63,116–118,144],

§6 Why do semaphoronts to which specific hypotheses *xus* and *yus* refer have character $x(1)$ in contrast to $x(0)$ as seen among individuals to which other specific hypotheses (*aus*, *bus*, etc.) refer?

The abductive inference responding to this question **§6** has the form,

§7 • *Background knowledge b*, e.g., assumption that observation statements are true

- *Phylogenetic theory:*

If character $x(0)$ exists among individuals of a reproductively isolated, gonochoristic or cross-fertilising hermaphroditic population and character $x(1)$ originates by mechanisms a, b, c… n, and becomes fixed within the population by mechanisms *d*, *e*, *f*… *n* (= ancestral species hypothesis), followed by event(s) *g*, *h*, *i*… *n*, wherein the population is divided into two or more reproductively isolated populations, then individuals to which descendant species hypotheses refer would exhibit *x*(1).

• *Observations (effects):*

Individuals to which specific hypotheses *xus* and *yus* refer have character *x*(1) in contrast to *x*(0) as seen among individuals to which other species hypotheses (*aus*, *bus*, etc.) refer.

• *Causal conditions (phylogenetic hypothesis Xus):*

Character *x*(1) originated by some unspecified mechanism(s) within a reproductively isolated population with *x*(0), and *x*(1) became fixed in the population by some unspecified mechanism(s), followed by an unspecified event(s) that resulted in two or more reproductively isolated populations.

Notice the differences between why-questions in **§4** and **§6**, leading to inferences of specific and phylogenetic hypotheses **§5** and **§7**, respectively. The premise, *Phylogenetic theory*, in **§7** differs from the *Species theory* in **§5** in that the former not only considers novel character origin and fixation, but also subsequent population splitting (‘speciation;’ Figure 2H). Like the *Species theory*, the *Phylogenetic theory* is intentionally vague regarding causal specifics. This reflects the absence of causal details that go into the implementation of phylogenetics algorithms, which leads to the minimal explanatory content in phylogenetic hypotheses implied by phylogenetic trees or cladograms [42,43,50,63,116]. Similar to the inference of a specific hypothesis, the *Phylogenetic theory* is limited to gonochoristic or cross-fertilising hermaphroditic organisms since population splitting events are not relevant to asexually reproducing, obligate parthenogenetic, or self-fertilising hermaphroditic organisms [115,116].

Consistent with the necessary presupposition that observation statements are true (cf. *Why-questions*), which is part of the *Background knowledge*, explanations of homologous characters should be pursued in a manner that extends the presupposition as much as possible to inferred explanatory accounts. In other words, a common cause theory is applicable in **§7**, which the *Phylogenetic theory* offers. For the purposes of this example, the premise, *Observations (effects)*, presents only one set of observation statements. This premise typically includes other relevant characters, as are conveyed in a standard character data matrix. The matrix implies one’s why-questions as well as the totality of observation statements comprising the *Observations (effects)* premise [43,63,144]. The conclusion, *Causal conditions*, implied by phylogenetic trees or cladograms, is the result of applying the *Phylogenetic theory* to *Observations (effects)* as fully as possible, in answer to why-questions of the form in **§6**. The limited causal details in the conclusion (Figure 4) are consequences of the minimal causal specifics offered by the theory. Phylogenetic trees are tantamount to ‘explanation sketches’ [8] in that they lack causal specifics that would qualify such diagrams as reflecting full explanatory accounts. As part of the ampliative nature of abduction, premises can lead to a single or multiple, mutually exclusive conclusions.

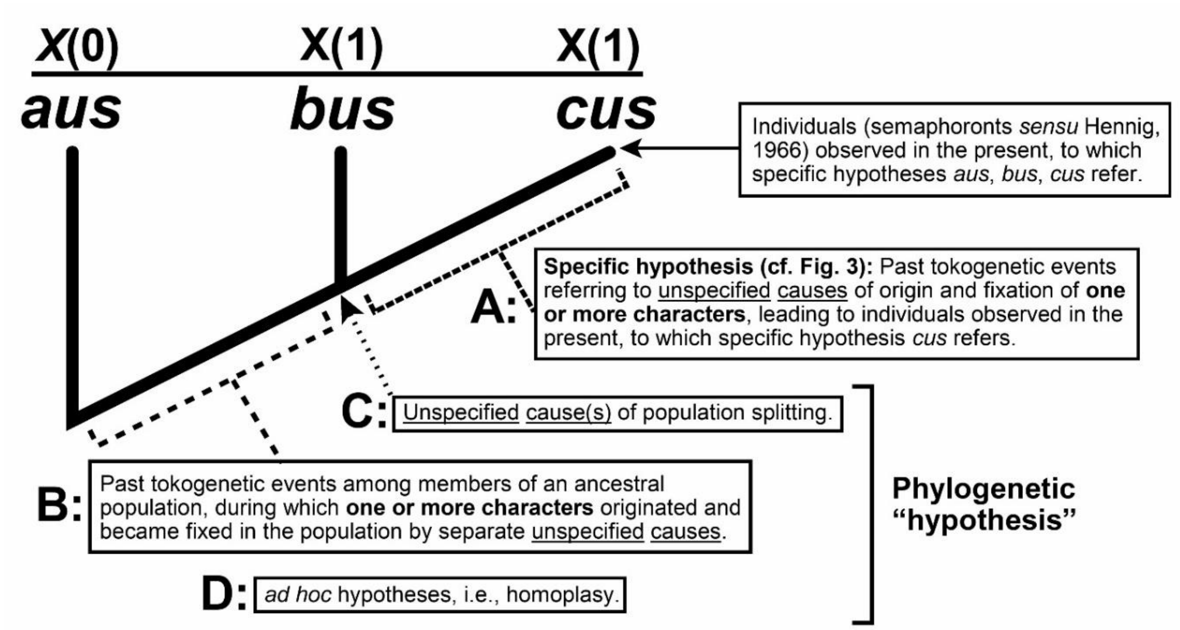

Figure 4. Explanatory hypotheses implied by cladograms or phylogenetic trees. Two classes of hypotheses are shown: (**A**) specific and (**B–D**) phylogenetic, causally accounting for homologous characters. Inferences of specific hypotheses are distinct from phylogenetic inferences, cf. [63,113,115–117], but both offer vague explanatory accounts. Modified from [43,63,64].

It was noted earlier that a phylogenetic tree or cladogram is referred to as a phylogenetic *hypothesis*, but these graphic devices always imply composite hypotheses that entail a minimum of three classes of explanatory hypotheses (Figure 4): previously inferred specific hypotheses (cf. **§5**; Figure 4A), and two classes of hypotheses derived from the premises in **§7**, i.e., novel character origin/fixation among members of ancestral populations (Figure 4B), and population splitting events ('speciation') (Figure 4C). An additional, *ad hoc* class of hypothesis, homoplasy, is often inferred (Figure 4D).

Recall earlier (**2. Root of the Problem: Filling the Inferential Void in Systematics)** that with phylogenetic inference involving abductive reasoning, there are notable implications for phylogenetic methods called parsimony, likelihood, and Bayesian. Parsimony is a criterion for selecting among hypotheses that have been previously inferred by way of abduction. What is often called a 'parsimony method' is just abduction that maximizes explanatory hypotheses by way of common causes, e.g., the *Phylogenetic theory* in **§7**. The algorithm performs abductive reasoning emulating examples in **§1** and **§7** such that the inference explains as fully as possible homologous characters. In other words, minimizing separate causal events for what are assumed to be the same characters is in accordance with assuming the truth of one's observation statements, as discussed earlier in relation to why-questions. Likewise, so-called likelihood and Bayesian phylogenetic inferences are abductive, but unlike the inference in **§7**, stochastic evolutionary processes are part of the premises. Distinct from the premises in **§7**, there is the implication that observation statements of homologous characters must be presumed not to be necessarily the same. For instance, "Modeling character change as a continuous-time Markov process has a number of advantages. First, the number of character state changes increases with time or substitution rate, in contrast to the parsimony method [*sic*], which allows at most one character-state transformation along a single branch of a phylogeny" [185] (p. 133). The difficulty is that this approach necessitates potentially excessive and indiscriminate *ad hoc* hypotheses of homoplasy in order to causally account for what are originally interpreted as homologous characters. This insulates phylogenetic hypotheses from legitimate testing even more so than when common-causes hypotheses are inferred [42,48,60]. The only solution is that at least some observed characters, per one's why-questions, **§6**, should be regarded as *different*, based on one's background knowledge of stochastic character evolution. That background knowledge would, however, be taken into consideration *prior to* inferences of phylogenetic hypotheses, not *within* the inferences. In other words, original observation statements would need to be revised according to one's background knowledge regarding evolutionary causes *prior to* inferring hypotheses. Otherwise, premises of abductive inferences would be contradictory to one's presumed true observation statements and why-questions [50]. Accepting the assumption that initial observation statements of similarity, i.e., homologues, are erroneous first requires renaming those *homologous* characters as *different* characters before proceeding with explaining the *revised* observation statements that accord with one's background knowledge. These revised observation statements then become part of background knowledge that subsequently dictate the premises of abductive inferences. For instance, the background knowledge allowing for causally accounting for aligned sequence data would need to be altered to reflect revised observation statements [50]:

§8 Revised background knowledge:

(a) observation statements of homologous nucleotides, are initially assumed true, per alignments of sequence data;

(b) rates of sequence substitution are taken into consideration;

(c) per (b), the assumption of truth of observation statements in (a) is not necessarily correct;

(d) per (b) and (c), observation statements are revised such that apparent homologous nucleotides or amino acids are renamed as *different* observation statements where applicable to reestablish true observation statements.

With this accommodation of background knowledge, the *Phylogenetic theory* in **§7** would remain in use to infer phylogenetic hypotheses maximizing common causes, since the actions in **§8** ensure that phylogenetic inferences once again causally account for homologous characters.

To summarize, while there has been a 60+ year tradition in systematics of claiming phylogenetic hypotheses can be inferred by methods called parsimony, likelihood, or Bayesian, the actual form of inference is abductive. Pursuant to the objective of such inferences being the causal explanation of homologous characters, background knowledge presupposing observation statements are true leads to inferences that maximize common-cause explanations, thus minimizing *ad hoc* hypotheses of homoplasy. Calling that background knowledge into question would need to be addressed prior to inferring hypotheses, subsequent to which revised homologous characters would resume being explained via a common-cause phylogenetic theory.

4. The Case Against ASR/CM

The topics addressed in previous sections are necessary prerequisites laying the foundation for presenting a novel critique of ASR/CM. Some of these prerequisites were applied in my original critique of character mapping [19], pointing out relevance of the RTE to phylogenetic inference as an instance of abductive reasoning. In this section the RTE is revisited to highlight that while its original intent in the philosophical literature pertained to inductive reasoning, the case can be made that the requirement applies to phylogenetic inferences in general and is a specific criterion showing ASR/CM is not sound reasoning. After addressing the RTE, a new argument is presented, complimentary to the RTE, that further denies the scientific utility of ASR/CM.

4.1. Update on the RTE as a Critique of ASR/CM

The RTE in relation to systematics and abductive reasoning was briefly outlined earlier (**2. Root of the Problem: Filling the Inferential Void in Systematics**), specifying that since the requirement applies to non-deductive reasoning, it should apply to abduction. As the RTE is a strong argument against ASR/CM, clarification of this point relative to both abductive and inductive reasoning is in order since some nuances were not made clear in my previous treatments of the RTE [18,19] when applied to systematics. I noted earlier that original reference to the RTE by Carnap [5,6], emphasis original) was purposefully restricted to inductive reasoning, meaning that the requirement ensures that all *relevant test evidence* is taken into consideration when assessing credibility of, or support for a hypothesis: "'*Requirement of total evidence*': in the application of inductive logic to a given knowledge situation, the total evidence available must be taken as basis for determining the degree of confirmation" [6] (p. 211). Hempel [108] (p. 128, emphasis original) offers this description of the RTE:

> "When two sound inductive arguments thus conflict, which conclusion, if any, is it reasonable to accept, and perhaps act on? If the available evidence includes the premises of [two different] arguments, it is irrational to base our expectations concerning the conclusions exclusively on the premises of one or the other of the arguments; the credence given to any contemplated hypothesis should always be determined by the support it receives from the *total* evidence available at the time ... What the requirement of total evidence demands, then, is that the credence given to a hypothesis *h* in a given knowledge situation should be determined by the inductive support, or confirmation, which *h* receives from the total evidence *e* available in that situation."

Salmon [13] (p. 76, emphasis original) expresses a similar view:

> "Given that the degree of confirmation of hypothesis *h* on evidence *e* is *p*, and given also the truth of *e*, we are not allowed to infer *h* even if *p* is very near one. Rather, we must use our inductive logic according to certain definite rules of applications. First, there is the requirement of total evidence. If *e* is the evidence statement we are going to use, it must incorporate *all* relevant available evidence. This is an important respect in which inductive logic differs from deductive."

More recent philosophical treatments of the RTE have continued to emphasize its application in relation to induction [20,186,187]. As noted earlier, the RTE is automatically satisfied in deduction, meaning the premises contain all relevant premises.

An important aspect of the RTE is Carnap's [5,6] view on relevant evidence. As premises of any inference constitute evidence for a conclusion based on those premises [12], evidence is relevant if it has either a positive or negative impact on the conclusion [5,6,18,188]. Of course, Carnap's [6] (p. 347, emphasis original) reference to relevance pertains to hypothesis confirmation via test evidence: "If the posterior confirmation $c(h, e \,.\, i)$ is higher than the prior confirmation $c(h, e)$, we shall say that the additional evidence *i* is ***positively relevant*** or, simply, ***positive*** to the hypothesis *h* on the evidence *e*… If it is lower, we shall say that *i* is ***negatively relevant*** or *negative* to *h* on *e*…." I will point out later in this section that a somewhat similar notion of evidential relevance should apply to phylogenetic inference and the critique of ASR/CM.

Outside of systematics, the RTE has not been associated with abductive reasoning in the philosophical literature. The first specific application of the requirement to abduction was by me in relation to phylogenetic inference [18]. The lack of attention given to the RTE relative to abduction appears to have two reasons. As mentioned earlier (**2. Root of the Problem: Filling the Inferential Void in Systematics**), for much of 20th century philosophy of science, especially after the death of Charles Sanders Peirce in 1914, abduction was relegated to being a psychological manifestation that had no logical interpretation. For instance, in his characterization of science, Reichenbach [105–107,189] coined the phrases, *context of discovery* and *context of justification*. The context of discovery includes actions of inferring hypotheses and theories, while the context of justification involves empirical testing of propositions. Reichenbach [105] (p. 36) makes clear his view that the context of discovery lies beyond the 'logic of science:'

> "If we want to construct a philosophy of science, we have to distinguish carefully between two kinds of context in which scientific theories may be considered. The context of discovery is to be separated from the context of justification; the former belongs to the

> psychology of scientific discovery, the latter alone is to be the object of the logic of science. The confusion of the two kinds of context has become the root of many a misinterpretation of the procedure of science. I confess that the remarks of Peirce concerning the construction of scientific theories, [...] seem to me to suffer from the same confusion. I admire Charles Peirce as one of the few men who saw the relations between induction and probability at an early time; but just his remarks concerning what he calls ‘abduction’ suffer from an unfortunate obscurity which I must ascribe to his confounding the psychology of scientific discovery with the logical situation of theories in relation to observed facts.”

Reichenbach’s animosity toward abduction and relegating the context of discovery to psychology is echoed by Popper [29] and Hempel [108]. It was not until Hanson’s [76] *Patterns of Discovery* that abduction began to regain recognition as fundamental to scientific inquiry. The second reason the RTE has not been associated with abduction might be because traditional emphasis on the requirement has centered on test evidence and inductive reasoning, not effects prompting inferences of hypotheses. Plus, inferring explanatory hypotheses of common causes either outside of, or within biology have likely involved effects that do not raise awareness of the risk of producing contradictory hypotheses as represented by phylogenetic hypotheses inferred from partitioned data.

The first consideration of the RTE in relation to phylogenetic inference was by Kluge [122]. What is notable is that Kluge [122] (p. 9, emphasis original) incorrectly attempts to apply the RTE under the view that homologous characters serve as test evidence: “Cladists take the position that congruent characters confirm a phylogenetic hypothesis, *provided they are independent*. The more independent congruent characters there are for a clade, the better supported [sic] it is as a phylogenetic hypothesis.” The idea that character congruence is a test of phylogenetic hypotheses has its origin with Hennig [172], subsequent to which this notion of testing was incorrectly connected to Karl Popper [190,191]. Wheeler [192] (p. 73) echoes Kluge’s position at the same time associating it with Popper’s [192] ‘severity of test’ in relation to falsification: “The idea of Total Evidence Analysis, for instance Kluge (1989), is grounded in severity of test. The greater the amount and diversity of evidence brought to bear on a question, the greater the opportunity for falsification and the more severely the hypothesis is tested.” Homologous characters do not have the capacity to serve as test evidence when what is being tested are the various causal claims (cf. Figure 4) implied by phylogenetic hypotheses inferred to explain those characters [42,48,165]. Others, e.g., [31,119] incorrectly associate the RTE with the use of parsimony in phylogenetic inferences.

While the original intent of the RTE was to establish a standard for rational acceptance of theories and hypotheses on the basis of available relevant test evidence, I [18,19] have shown that the RTE also applies to abduction, at least in the context of some classes of systematics hypotheses. Further clarification, however, of the requirement’s importance for inferences of specific and phylogenetic hypotheses are in order. I remarked earlier [*3.5. Inferences of Specific (Species) Hypotheses*] that the RTE applies to inferences of specific hypotheses (Figure 3). The same applies to phylogenetic hypotheses in that organisms are integrated wholes, and explaining one class of characters is relevant to explaining other classes of characters [18,19], as is evident by the fact that separately inferred phylogenetic hypotheses can be contradictory. As a matter of non-deductive reasoning, it would be irrational to accept either set of conclusions. The same problem applies to ASR/CM since fitting characters onto a previously inferred phylogenetic tree means the mapped characters are denied explanations in conjunction with characters explained in the original inference. This compromises plausibility of both the original hypotheses and purported hypotheses obtained via ASR/CM. I [19] have also noted that inferring separate sets of phylogenetic hypotheses from partitioned data for the same organisms suffers the same problem due to the incoherence of comparing tree topologies. Added to this is the consequence that attempting to explain characters through ASR/CM is a faulty attempt at abduction; a consideration that will occupy the new critique presented later (cf. *4.2. ASR/CM Relies on an Inappropriate Premise*).

The criterion of evidential relevance, mentioned earlier in relation to application of the RTE to induction, also applies to abduction. Taking relevance into account, a more general conception of the RTE can be characterized similar to that described by Neta [20] (p. 91): “All that the requirement of total evidence says is that one’s confidence in a hypothesis must be proportional to the support that that hypothesis receives from one’s evidence....” Support in this more general sense refers to the premises that warrant a conclusion, regardless of the type of reasoning involved. Rather than confidence in a hypothesis, the appropriate criterion for abduction would be plausibility, since confidence cannot be ascribed to untested hypotheses. An appropriate connotation of the RTE applied to abduction might be, ‘The plausibility of an abductively inferred hypothesis is proportional to the inclusion of all *relevant effects* to be explained.’ Using this interpretation of the RTE to infer phylogenetic hypotheses, there are two issues that require careful reflection when thinking of homologous characters being relevant. On the one hand, there is the standard assumption in systematics, discussed earlier (cf. [144]), that different characters are independent of one other, such that separate hypothesized events of character origin and subsequent fixation in ancestral populations are inferred. This was addressed earlier in the case of two or more characters explained via composite specific hypotheses (**§5**; Figure 3: hypotheses h_1 and h_2), and also applies to phylogenetic hypotheses that stipulate novel character origins and fixation (**§7**; Figure 4B). On the other hand, inclusion of independent characters in phylogenetic inferences also involve hypothesized population splitting events (**§7**; Figure 4C), meaning these characters are *relevant* to one other in the case of population splitting because exclusion of any of them from the inference will compromise plausibility of the composite phylogenetic hypothesis. For instance, partitioned data sets for the same group of organisms will lead to separate sets of phylogenetic hypotheses, with the possibility of different phylogenetic tree topologies, indicating different hypotheses of population splitting events [19]. Those separate inferences also run the risk of producing hypotheses of character origin/fixation that would be different had the two sets of characters been combined into a single inference. The plausibility of each separate phylogenetic hypothesis should be seen as less than that of the phylogenetic hypothesis inferred from combined observations. I [18] (p. 330) made a similar argument:

> “Just as the context in which we describe the properties of organisms in the present is by way of the fact that all objects exhibit discernable features…, our inferences of historical events accounting for observed properties of individual organisms, semaphoronts, in the present must be considered in terms of past whole organisms. In fact, it is the matter of evidential relevance that establishes the importance of the RTE in phylogenetic inference, as well as the fact that the requirement cannot be ignored.”

The more traditional description of the RTE described earlier was sufficient for instances of induction, where inclusion of all relevant test evidence should be taken into account for judging hypothesis confirmation. By clarifying importance of the RTE for all non-deductive reasoning by emphasizing premises as relevant test evidence in induction and all relevant effects in relation to hypothesis plausibility in abduction, the RTE remains a strong argument not only against inferences of phylogenetic hypotheses from partitioned data but also against ASR/CM.

4.2. ASR/CM Relies on an Inappropriate Premise

Beyond the RTE precluding ASR/CM being a rational means of inferring explanatory hypotheses of homologous characters, the progression of topics discussed thus far provide the foundation for identifying another shortcoming of the method. We saw earlier the basic structure of abductive reasoning used to infer phylogenetic hypotheses as the means to answer particular why-questions regarding characters instantiated by organisms (cf. **[6,7]**). This section will show that ASR/CM, as an attempt to infer phylogenetic hypotheses, is indefensible because it requires an epistemically meaningless premise, inevitably leading to logically and scientifically specious hypotheses.

Instances of ASR/CM usually take one of two general forms. The most common being ASR *sensu stricto*, relies on phylogenetic trees previously inferred from sequence data to fit or 'optimize' homologous phenotypic characters onto trees under the pretense of explaining those characters using stochastic methods [21,22]. Examples can be found applied to microbes [193], invertebrates [194–209], vertebrates [26–28,205,210–228], and plants [23,229–233]. To a lesser extent there is the more traditional character mapping approach to fit characters on a previously inferred tree by applying 'parsimony,' meant to maximize mapped phylogenetic hypotheses of common causes [234–249]. ASR/CM methods are therefore constrained by a tree topology inferentially irrelevant to the mapped characters. Such reconstructions are intended to present hypotheses of character origins and fixation, associated with population splitting events coopted from a previous, unrelated phylogenetic inference. Algorithmic methods specifically designed to enable ASR have been reviewed by Revell [22]. Details regarding the manner in which these applications produce results are not relevant to the present critique since the problem discussed here transcends all attempts to use ASR/CM.

Consider once again the quote from Revell [22] (p. 1, emphasis original) given earlier (**1. Introduction**), "Ancestral state reconstruction falls within the domain of phylogenetic comparative methods… typically employed *downstream* of phylogenetic inference to *test* hypotheses about evolution based on a *tree*, and often in combination with trait data for the taxa of that tree." This characterization conflates inferences of hypotheses with the testing of those hypotheses; a long-standing predicament in systematics, so Revell's description needs some unpacking. It was discussed earlier (cf. *3.3. Forms of Reasoning*) that operational relations between inferences of hypotheses by way of abductive reasoning (cf. **[§1]**, **[§5]**, **[§7]**), the prediction via deduction of potential test evidence as expected consequences if a hypothesis is true (cf. **[§2]**), and that the act of testing, i.e., seeking and reporting results of that test evidence, is inductive (cf. **[§3]**). Granted, while we can acknowledge that phylogenetic inference is abductive, we have to keep in mind the intent is not to produce phylogenetic trees, but rather explanatory hypotheses implied by those trees (e.g., Figure 4), causally accounting for the characters that are premises in the inference (cf. **[§5]**). To the contrary, Revell [22] (see also earlier quote by Cockx et al. [24]) suggests ASR is a test "about evolution based on a tree, and often in combination with trait data for the taxa of that tree." Does ASR test evolutionary or phylogenetic hypotheses? Obviously not, given what is required to test explanatory hypotheses, summarized in **[§2]** and **[§3]** [42,48,60]. As illustrated in Figure 4, phylogenetic hypotheses offer claims that particular characters originated in reproductively isolated ancestral populations (Figure 4B), subsequent to which there was a population splitting event (Figure 4C), which causally accounts for individuals in the present exhibiting the homologous characters being explained. And additional *ad hoc* hypotheses of homoplasy are possible (Figure 4D). Since phylogenetic hypotheses are, by definition, composite hypotheses, testing requires acknowledging that there are at least three different classes of hypotheses subsumed under any phylogenetic hypothesis, and each of those hypotheses require separate events of testing. The mechanics of testing then require predicting that if the hypothesized causal events occurred, then effects, as predicted test evidence, should be observed that have the lowest probability of occurrence if those events did not occur. In other words, predicted test evidence ideally should be effects that could only be produced by the hypothesized causes. Since phylogenetic trees offer almost no specifics regarding causal events, testing cannot proceed until the subsidiary hypotheses are fully filled out as complete explanatory accounts that enable proper predictions of potential test evidence. In the absence of those causal details and the fact that ASR is not logically sound reasoning, there can be no opportunities for testing via ASR, much less after the fact.

If it is the case that ASR "falls within the domain of phylogenetic comparative methods… typically employed *downstream* of phylogenetic inference" [22] (p. 1), what would the formal structure of such an inference look like? Following the examples of phylogenetic inference in **[§1]** and **[§5]**, ASR/CM is represented by the following abduction:

[§9] • *Background knowledge b*, e.g., assumption that observation statements of homologous characters are true

- *Phylogenetic theory* (whether using common cause or a stochastic approach is irrelevant in this instance)
- *Observations (effects)*, homologous phenotypic characters among individuals to which particular specific hypotheses refer
- *Phylogenetic tree*, (*dus* (*cus* (*aus*, *bus*))), previously inferred to explain sequence data
- Phenotypic characters mapped on phylogenetic tree (*dus* (*cus* (*aus*, *bus*)))

Notice that in addition to the first three premises, ASR/CM requires the additional premise, shown in bold, of a phylogenetic tree previously inferred to purportedly explain sequence data. This latter premise ultimately determines the conclusion, in the form of phenotypic characters mapped on the tree. The conclusion is little more than a vague representation of supposed explanatory hypotheses, akin to those hypotheses typically inferred by proper abduction, i.e., **[§1]**, **[§7]**.

Regarding the phylogenetic tree as a premise in **[§9]**, two distinct problems are apparent that immediately indicate ASR/CM is logically unsound abductive reasoning. The first is that the phylogenetic tree is nothing more than a branching diagram that is not germane to explaining the phenotypic characters. To reiterate what was discussed earlier (cf. *3.6. Inferences of Phylogenetic Hypotheses*) and summarized in Figure 4, a phylogenetic tree implies a set of explanatory hypotheses. The tree diagram by itself is an epistemically empty contrivance when used as a premise, lacking relevance to characters not originally used to infer hypotheses implied by that tree. The second problem is that regardless of how phenotypic characters are 'optimized,' 'fitted,' or 'mapped' onto a preexisting tree, that action cannot lead to a conclusion that imparts any explanatory statements since the tree is the product of a previous inference intended to explain a set of sequence data, not the phenotypic characters introduced after the fact. The conclusion, in the form of mapped characters, is unequivocally guaranteed to be faulty as an explanatory device. The only rationally viable solution, notwithstanding very significant limitations associated with attempting to explain sequence data [43,50], discussed next, is to combine all classes of relevant characters as premises and infer a new set of phylogenetic hypotheses, per the RTE.

Beyond satisfying the RTE, there are two additional caveats to consider in addition to avoiding ASR/CM. The first, discussed earlier, is the assumption as part of one's background knowledge that observation statements of homologous characters are true (cf. *3.2. Why-Questions*; **[§1]**, **[§5]**, **[§9]**). Without such an assumption there could be no why-questions that lead to the pursuit of causal inferences. Assuming observation statements of homologous characters are true then answering why-questions regarding those observations necessitates an inference using a phylogenetic theory of common causes [50] (cf. **[§5]**), as opposed to a theory of stochastic change, which is contrary to one's background knowledge. I noted earlier, cf. **[§8]**, that if initial homologous characters are deemed incorrect because rates of sequence substitution are required, this would mean an empirical basis for renaming specific homologous nucleotides or amino acids as different due to convergence would be needed prior to proceeding with inferring phylogenetic hypotheses **[§8**(d)**]** [50]. With those modifications, the common cause phylogenetic theory would still be applied, as shown in **[§7]**. I am unaware of any empirical criteria that can establish which among homologous nucleotides or amino acids should be regarded as convergent prior to abductively inferring explanatory hypotheses. The second stipulation for satisfying the RTE, which has been consistently overlooked when considering causally accounting for homologous nucleotides or amino acids, is that it is incumbent to distinguish between those sequence data to be explained by genetic drift versus fixation due to natural selection [43]. The distinction is required since drift can directly explain homologous nucleotides or amino acids, but selection can only be an indirect causal factor due to the fact that fitness differences among individuals are not directly caused by these molecules. Rather, differential fitness will be determined by higher level phenotypic expressions. It is by way of the phenomenon of downward causation that selective pressure for certain phenotypes will indirectly determine what sequence data will eventually become fixed in a population. Downward causation in relation to evolutionary biology was first discussed by Campbell [250] (p. 180): ''Where natural selection operates through life and death at a higher level of organisation, the laws of the higher-level selective system determine in part the distribution of lower-level events and substances.'' Subsequently, downward causation has received increasing attention, e.g., [251–273], but its relevance and implications for explaining sequence data via phylogenetic hypotheses has only recently been considered [50]. Given the indirect causal accounting for particular sequence data by way of downward causation, those data would be removed from any abductive inference in lieu of the associated phenotypic characters also included in the inference. The upshot is that ASR/CM neither infers nor tests explanatory hypotheses for phenotypic characters. In every instance, results from such methods cannot be philosophically or scientifically justified.

5. Conclusion

Scientific inquiry is founded in part on principles regarding the operational relations between non-deductive and deductive reasoning. While the recent history of systematics, especially due to the writings of Karl Popper, led to heightened concerns about the testing of phylogenetic hypotheses, the actual treatment of types of reasoning leading to inferences and subsequent testing did not materialize until the early 2000's, when abductive, deductive, and inductive forms of reasoning and their operational relations were clearly articulated. But this recognition has remained largely peripheral to the previously established methodological schools of thought wherein phylogenetic inference is incorrectly referred to as 'parsimony,' 'likelihood,' or 'Bayesian.' This paper has shown one of the consequences of the failure to recognize that inferences of phylogenetic hypotheses is only accomplished by abduction, not via parsimony or inductive reasoning: that violating the RTE and mapping phenotypic characters on a phylogenetic tree originally inferred to account for sequence data is logically unsound. The development of ASR/CM is guaranteed to produce results that compromise the standing of systematics as a science, made worse by the fact that its increasing popularity inevitably leads to spurious results. Evaluating the veracity of inferential methods in systematics in light of abduction should be an ongoing priority.

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