

# Essentialism, History, and Biological Taxa

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## Abstract

de Queiroz (1995), Griffiths (1999) and LaPorte (2004) offer a new version of essentialism called “historical essentialism”. According to this version of essentialism, relations of common ancestry are essential features of biological taxa. The main type of argument for this essentialism proposed by Griffiths (1999) and LaPorte (2004) is that the dominant school of classification, cladism, defines biological taxa in terms of common ancestry. The goal of this paper is to show that this argument for historical essentialism is unsatisfactory: cladism does not assume that relations of common ancestry are essential attributes of biological taxa. Therefore, historical essentialism is not justified by cladism.

*Keywords:* historical essentialism, cladism, biological taxa, natural kinds

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## 1. Introduction

Traditionally, philosophers have treated biological taxa as natural kinds with kind-specific essences. This view has been challenged by various types of arguments by both biologists and philosophers (Ereshefsky, 2001). One of the main objections to the position that biological taxa are kinds is that membership in species and higher taxa depend on *history* and that natural kinds cannot be historically delimited (Hull, 1978; Ghiselin, 1974). As Hull and Ghiselin articulate this objection, natural kinds are not historically delimited because their members are not spatiotemporally restricted. For instance, an atom is an instance of the kind gold if it has atomic number 76, no matter its time and location in the universe. However, if we follow Darwin’s lead in thinking that classification of organisms should be genealogical,

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then the members of a taxon become spatiotemporally restricted: “in the typical case, to *be* a horse one must be *born* of horse” (Hull, 1978, p. 349). As an alternative to the view that biological taxa are natural kinds, Hull and Ghiselin claim that biological taxa should be thought as *individuals*. In short, their insight is that organisms are conspecific not because they necessarily share a certain property, the taxon’s essence, but because they are (spatiotemporally restricted) parts of the same species.<sup>1</sup>

The philosophers Joseph LaPorte (2004) and Paul Griffiths (1999) find this objection unconvincing. They think that natural kinds are not historical only if we subscribe to the view that kind-essences are intrinsic properties. According to them, natural kinds can be historically delimited and, for this reason, biological taxa can be understood as natural kinds. In order to show that, LaPorte and Griffiths propose a version of essentialism called *historical essentialism*, according to which certain ancestor-descendant relationships are essential features of biological taxa. In their view biological taxa can be natural and, yet, historically delimited.

Nevertheless, showing that natural kinds can be historical is not the only reason LaPorte and Griffiths present in favor of historical essentialism. Most importantly, they think that historical essences address an important issue about biological taxa. They claim that essences explain why organisms belonging to the same taxon tend to share certain features. As an example, consider LaPorte’s comment on polar bears:

A lot is explained by an object’s being a polar bear. That it is a polar bear explains why it raises cubs as it does, or why it has extremely dense fur, or why it swims long distances through icy water in search of ice floes. ... The polar bear kind is a useful one for providing significant explanations. It is a natural kind. (LaPorte, 2004, p. 19).

In a similar fashion, Griffiths justifies his appeal to essences on the grounds that generalizations involving taxon names have “counterfactual force”:

A hierarchical taxonomy based on strict phylogenetic principles will collect more of the correlations between characters, from molecular to behavioral, than any other taxonomy we know how

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<sup>1</sup>See Ereshefsky (2001, 2010a) for further details.

to construct. Such a taxonomy will group organisms into natural kinds because it will predict with considerable force many properties of individuals (Griffiths, 1999, p. 222).

LaPorte and Griffiths assume that it is not a matter of coincidence that members of the same taxon tend to share certain similarities. Instead, they claim that all members of a taxon – past, present, or future – are inevitably alike in some respect (e.g., in respect to how they raise their cubs). That’s why modal considerations are relevant to historical essentialists. If historical essences were defined as properties of existing organisms only, then historical essences couldn’t explain why future (and past) members of a taxon tend to be alike. But since historical essences are supposed to be explanatory, they have to be construed as properties of any *possible* member of a taxon.

In this paper, my focus is not on the issue of whether historical essences have an explanatory import. Rather, my goal is to reject the argument LaPorte and Griffiths put forward for the existence of historical essences. The main argument used by LaPorte and Griffiths in favor of historical essentialism is that the dominant school of classification, cladism, defines biological taxa in terms of ancestor-descendant relations. Section 2 outlines this argument for historical essentialism; in sections 3 and 4 I argue that cladism does not support historical essentialism. The main motivation for thinking that cladism justifies historical essentialism is the assumption that cladists define biological taxa in terms of genealogical relations. However, in section 3 I point out that an influential group of cladists, *pattern cladists*, do not define biological taxa in terms of genealogical relations but in terms of characters of individual organisms. I use this fact to make the point that citing cladism alone is not sufficient to warrant the existence of historical essences; historical essentialists must also provide a further argument showing why we should favor *process cladistics*, a version of cladistics that defines biological taxa in terms of genealogical relations. Nevertheless, this is not the only problem historical essentialists face. Historical essentialism has been defined by LaPorte and Griffiths as the view that sharing a certain ancestor is an essential attribute of biological taxa (section 2). As I argue in section 4, the use of genealogical relations by process cladists does not warrant historical essentialism. As we shall see, process cladism sorts taxa into groups but does not identify which taxon is the most recent common ancestor of a group. For these reasons, historical essentialism is not justified by cladistics, be it pattern or process cladistics.

## 2. Biological Taxa and Historical Essences

Suppose that in the actual world the same group of organisms is picked out by membership conditions formulated in terms of genealogy (e.g., descent from a common ancestral species) and in terms of certain morphological features. Even though both conditions demarcate the same group in the actual world, they may yield different groups in nonactual circumstances. In the debate about biological essentialism, the focus is on how membership conditions operate in both actual and nonactual circumstances. For essentialism is a view about what is the defining property of a taxon in *every* circumstance. A central reason nonactual circumstances are relevant for LaPorte and Griffiths is that essential features are supposed to explain why members of the same taxon, be them actual members or not, tend to share certain features. For instance, when LaPorte states that “A lot is explained by an object’s being a polar bear” (LaPorte, 2004, p. 19), he is not referring to existing polar bears only, but to any polar bear that *might* exist. The goal of this section is to introduce LaPorte’s and Griffiths’ views of biological essentialism. I start with LaPorte’s view.

### 2.1. LaPorte’s historical essentialism

A *clade* is a group of organisms containing a single common ancestor and all and only the descendants of that ancestor. For example, the zoologist Kevin de Queiroz defines “Mammalia” as “the clade stemming from the most recent common ancestor of horses and echidnas” (de Queiroz, 1995, p. 224). For de Queiroz, this definition assigns an essential property to the taxon Mammalia:

Just as it is logically necessary for a person to be married (and male) to be a husband, it is logically necessary for an organism to be part of the clade stemming from the most recent common ancestor of horses and echidnas to be a mammal (de Queiroz, 1995, p. 224)

De Queiroz uses two taxa, horses and echidnas, to serve as “reference points” in his definition of “Mammalia”. Call these reference points *specifiers*.<sup>2</sup> So, given a taxon  $x$  and its specifiers, de Queiroz’s notion of historical essence can be stated as follows:

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<sup>2</sup>See Sereno (2005) for a discussion about specifiers.

(QU) It's necessary that, for all  $y$ ,  $y$  is a member of the taxon  $x$  if and only if  $y$  descends from the most recent common ancestor of the specifiers of  $x$ .<sup>3</sup>

In a paper criticizing de Queiroz's (1992) view on taxon definition, Ghiselin (1995) makes the following remark:

As to counter-to-fact conditionals, it should be evident that the clade being named was the same clade that exists now, before the parts that are enumerated came into existence, and that it would be the same clade even if history had been somewhat different (Ghiselin, 1995, p. 221).

When applied to the taxon Mammalia, Ghiselin's remark implies that it is contingent, not necessary, that Mammalia ever gave rise to horses and echidnas. Thus, if Ghiselin is correct, then biological taxa do not contain historical essences as defined by de Queiroz (i.e., (QU)).

LaPorte (2004) proposes a version of historical essentialism that takes into consideration Ghiselin's aforementioned remark. LaPorte's argument comprises two premises: (1) biological taxa are clades; and (2) clades have historical essences. In favor of (1), LaPorte claims that "Cladists, who belong to the increasingly dominant cladistic school of systematics, identify higher taxa, like Mammalia (the mammals), Aves (the birds), or Serpentes (the snakes), with clades" (LaPorte, 2004, p. 11). In brief, LaPorte's argument for (1) is that practicing systematists endorse (1). Now I turn to LaPorte's justification for (2).<sup>4</sup>

LaPorte's (2004) formulation of the notion of historical essence is similar to de Queiroz's (1992; 1995). However, in order to deal with Ghiselin's remark, LaPorte adopts the following maneuver:

To make the essentialist lesson clear, I propose to *name* that group that happens, as a matter of contingent fact, to be the

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<sup>3</sup>This definition depends on the identity of the specifiers (i.e., horses and echidnas). For this reason, one might object that this definition is satisfactory only if the identity conditions of the specifiers are specified. De Queiroz' definition has been criticized for not providing such identity conditions. See Nixon and Carpenter (2000, 299-300) for an example.

<sup>4</sup>My goal of this section is to only present LaPorte's argument for historical essentialism without assessing it. The discussion about the validity of his argument is postponed until sections 3 and 4.

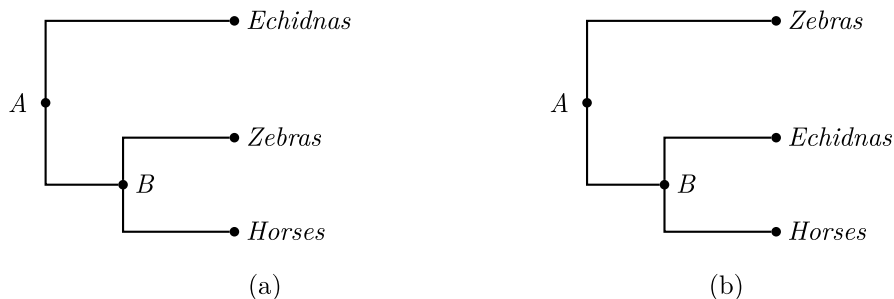
most recent ancestor common to both the horse and echidna. I give it the name ‘ $G$ .’ A cataclysm could have wiped out  $G$  before it ever gave rise to the horse or the echidna. But although it is contingent, not necessary, that  $G$  gave rise to the horse and the echidna, it is *necessary* that any organism belonging to the clade Mammalia be descendent from  $G$ , and that any organism belonging to the clade Mammalia be descended from  $G$  (LaPorte, 2004, p. 12).

LaPorte’s idea is that the specifiers of Mammalia (i.e. horses and echidnas) do not have to be necessarily the same. Rather, the invariant feature of Mammalia is the property of having  $G$  as the most recent ancestor. For LaPorte the specifiers are only necessary to fix the most recent ancestor of Mammalia in the actual world. Thus, LaPorte agrees with Ghiselin that it is a contingent matter that Mammalia gave rise to horse and echidnas. However, as opposed to Ghiselin, LaPorte insists that Mammalia contains an essential feature. In this way, given a clade  $x$  where  $G$  is the most recent common ancestor of the specifiers of  $x$  in the actual world, LaPorte’s notion of historical essence can be described as follows:

**(LP)** It’s necessary that, for all  $y$ ,  $y$  is a member of  $x$  if and only if  $y$  descends from  $G$ .

In order to illustrate the difference between de Queiroz and LaPorte’s notion of historical essence, consider two counterfactual situations represented by the trees in Figure 1. Suppose that the ancestral taxa  $A$  and  $B$  are distinct. Using de Queiroz’s definition of the taxon Mammalia, Mammalia represents the clade “ $A + B + \text{Echidnas} + \text{Zebras} + \text{Horses}$ ” on the tree (a), but the clade “ $B + \text{Echidnas} + \text{Horses}$ ” on the tree (b). However, according to LaPorte’s definition, these two groups identified by de Queiroz’s definition cannot be the same taxon Mammalia, because they have different most recent common ancestors in these two trees:  $A$  on the tree (a) and  $B$  on the tree (b). For de Queiroz we pick whatever the most ancestor of the specifiers is in a particular possible world:  $A$  on the tree (a),  $B$  on the tree (b). In contrast, for LaPorte, we pick the most recent ancestor of Mammalia in the actual world and then use this ancestry as an essential feature of Mammalia in nonactual circumstances.

Figure 1: Trees depicting different phylogenetic relations for the same taxa.



## 2.2. Griffiths' historical essentialism

According to Griffiths (1999), biological taxa contain historical essences because they are defined by relations of common ancestry. He illustrates his view with the following example:

Nothing that does not share *the historical origin* of the kind can be a member of the kind. Although Lilith might not have been a domestic cat, as a domestic cat she is necessarily a member of the genealogical nexus between the speciation event in which that taxon originated and the speciation event at which it will cease to exist. It is not possible to be a domestic cat without being in that genealogical nexus (Griffiths, 1999, p. 219, my emphasis).

From the above quote, we can extract the view that biological taxa contain historical essences in the sense that all the members of a taxon must share the same “historical origin”. The above quote thus suggests that sharing the same “historical origin” is an essential feature of biological taxa.

Griffiths' formulation of historical essence appeals to the notion of “historical origin”. Griffiths thinks that “historical origin” should be understood according to cladism: “It is not possible to be a domestic cat without being in that genealogical nexus. Furthermore, *cladistic taxa and parts and processes defined by evolutionary homology have no other essential properties*” (Griffiths, 1999, p. 219, my emphasis). In another quote, Griffiths says:

The fundamental kinds of the physical sciences ... have their properties because of their internal microstructure. But biological taxa, the other classic example of natural kinds, have their

causal homeostasis guaranteed quite differently. The most successful attempt to date to sort organisms into kinds which represent rich clusters of properties that can be relied upon to hold up in unobserved instances *is phylogenetic systematics . . . A cladistic classification of an organism or part allows reliable inferences about its structure, development, and behavior* (Griffiths, 1996, p. S5, my emphasis).

Thus, for Griffiths, sharing the same “historical origin” is an essential attribute of biological taxa.<sup>5</sup> Moreover, by using cladistics, Griffiths thinks that we can define “historical origin” in terms of common ancestry. In the following section I compare Griffiths’ view with LaPorte’s view on historical essences.

### 2.3. Griffiths and LaPorte on historical essences

Both LaPorte and Griffiths claim that common ancestry (as understood by cladistics) is an essential feature of biological taxa.<sup>6</sup> Moreover, they use the same line of argument for historical essentialism; namely that historical essentialism is true because of how the dominant school of classification, the cladistic school, defines biological taxa.<sup>7</sup> This argument for

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<sup>5</sup>One might point out that even though Griffiths occasionally makes claims containing modal locutions (as in the quoted passages), the whole modal business may well be less important to him than it is for LaPorte. Nonetheless, as discussed in the Introduction, Griffiths uses his theory about natural kinds to explain why certain generalizations about biological taxa have “counterfactual force”. For this reason, in addition to the passages I quoted, there is further evidence that Griffiths is concerned with nonactual circumstances.

<sup>6</sup>With respect to species taxa, LaPorte and Griffiths agree that sharing the same “historical origin” is at least part of the essence of species taxa. In particular, Griffiths states that, unlike higher taxa, species essences contain properties other than “belonging to a certain genealogical nexus”: “Taxa at the species level have rather more complex essences, because in their case these genealogical forces are supplemented by factors such as gene flow, selection, and developmental canalization” (Griffiths, 1996, p. S5). LaPorte thinks that a reasoning similar to the one applied to higher taxa can be applied to species taxa as well: “Mammalia and Aves are higher-level groups that contain many species. Similar reasoning reveals that *species* have essential properties on standard historical conceptions. Species, such as the horse species *Equus caballus* or the ostrich species *Struthio camellus*, necessarily stem from their ancestral groups just as clades do, though a species differs from a clade in that its descendants do not all have to belong to it” (LaPorte, 2004, p. 12).

<sup>7</sup>Using scientific theories to back up essentialist theories is a commonplace in contemporary philosophy. Kripke (1980) and Putnam (1975) proposed this sort of argument



historical essentialism can be formulated as a *modus ponens*: **(1)** if cladistically defined taxa satisfy (LP), then historical essentialism is true; **(2)** cladistically defined taxa satisfy (LP); therefore, **(3)** historical essentialism is true. A potential argument against historical essentialism can question the premise (1) – one might deny that scientific theories can count as evidence for essentialism for instance (see e.g. Mellor, 1977). This is *not* the type of argument I develop in this paper. Instead of rejecting (1), my goal is to show that the premise (2) is false; in my view, cladistics does not support the claim that sharing a *particular* most recent common ancestor is a defining feature of biological taxa.

### 3. Argument 1: process and pattern cladistics

In this section I distinguish two schools within cladistics: process cladism (subsection 3.1) and pattern cladism (subsection 3.2). Griffiths (1999) and LaPorte (2004) appeal to cladistics in order to justify their claim that biological taxa have historical essences. However, I will argue in this section (subsection 3.3) that pattern cladistics does not support historical essentialism. Hence, citing cladism alone does not justify historical essentialism. Cladism supports historical essentialism only if an additional premise is provided, namely that we have sufficient reason to accept process cladism and reject pattern cladism. However, as I argue in the next section (section 4), even if such an additional premise is provided, cladistics still does not support historical essentialism. But first we must give some background information concerning cladism.<sup>8</sup>

#### 3.1. Hennig's System

In order to describe his system of classification, Hennig (1966) distinguishes the following groups, based on their ancestry and descent (these examples are illustrated in Figure 2):

- A *monophyletic group* contains the common ancestor and all of its descendants. Examples: Vertebrata (Z + Y + X + lamprey + shark +

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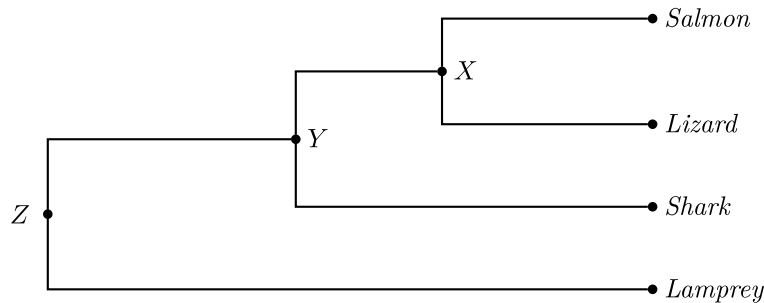
to defend essentialism about natural kinds. In addition to LaPorte and Griffiths, other philosophers of biology such as Okasha (2002) and Wilson et al. (2007) appeal to current biology to defend different versions of essentialism about biological taxa.

<sup>8</sup>Readers familiar with Hennig's cladism may skip Section 3.1 and proceed to Section 3.2.

salmon + lizard); Gnathostomata (Y + X + shark + salmon + lizard); and Osteichthyes (X + salmon + lizard).

- A *paraphyletic group* contains the common ancestor and some – but not all – of its descendants. Example: Pisces or “fishes” (Y + shark + salmon).
- A *polyphyletic group* contains some of the descendants of a common ancestor but not the common ancestor itself. Example: lamprey + salmon.

Figure 2: A tree depicting the ancestral-descendant relations between different taxa. The letters “X”, “Y”, and “Z” represent hypothetical ancestors of the terminal taxa. Adapted from Kitching et al. (1998, p. 11).

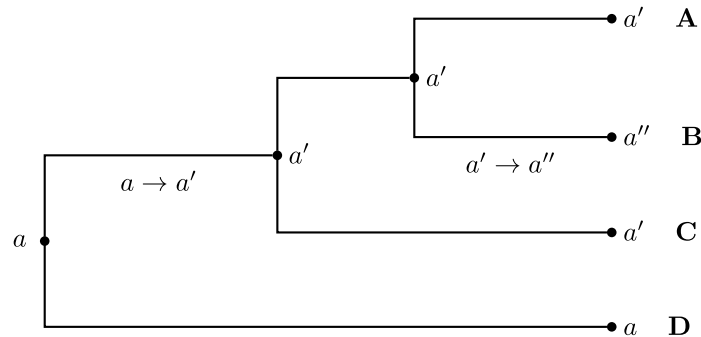


According to Hennig (1966), every higher taxon must be monophyletic. This supposition is a distinguishing feature of Hennig’s system in relation to other schools of taxonomy. Different from pheneticists such as Sokal and Sneath (1963), Hennig does not accept overall similarity as a criterion for delimiting biological taxa. And in contrast to evolutionary taxonomists such as Mayr (1969), Hennig does not allow paraphyletic groups – e.g. fishes in Fig. 2 (Y + shark + salmon).<sup>9</sup>

Monophyletic groups are discovered via analysis of characters. The characters used in cladistic analysis should be translated into discrete characters (e.g. “DNA sequences”) – as opposed to characters that vary continuously

<sup>9</sup>For further details about the different schools of taxonomy, see Ereshefsky (2001, ch. 2), Hull (2001), and Schuh (2000, ch. 1).

Figure 3: A tree representing the phylogenetic relations between the terminal taxa A, B, C, and D. The lower case letters  $a, a'$  and  $a''$  represent character states. The expression “ $x \rightarrow y$ ” represents a change in the character states among the members of the lineage from  $x$  to  $y$ .



(e.g. “leaf length”).<sup>10</sup> Each character in cladistic analysis has exclusive “states”. For instance, the character “mode of reproduction” has the states “viviparity” and “oviparity”.<sup>11</sup> However, not every character provides reliable evidence for inferring phylogenetic relations. For instance, if we consider a group containing a limpet, a barnacle, and a crab, even though barnacles and limpets look alike, the barnacle shares a more recent common ancestor with the crab than it does with limpets (Ridley, 1986, p. 4).

We should distinguish two types of character states: *plesiomorphies* are character states that are present in the common ancestor of the group of species under study; *apomorphies* are character states that evolved after the common ancestor, within the group of species under study. Apomorphies can be *autapomorphic* (unique to one group) or *synapomorphic* (shared between two or more groups). Consider the tree depicted in Fig. 3. For this tree, even

<sup>10</sup>The statement that “cladistics only use character with discrete variation” is a simplification. Discrete characters can be expressed in terms of characters that vary continuously. For example, the discrete state “leaves ovoid” can be described in the terms of a character varying continuously, the distance from the base to the widest point on the leaf (see Stevens, 1991; Thiele, 1993). For further details about character analysis in cladistics, see Kitching et al. (1998, ch. 2) and Schuh (2000, ch. 5).

<sup>11</sup>Hennig (1966) did not draw the distinction between character and states. This distinction only appeared with the rise of numerical approaches to taxonomy, in the middle of the 20th century (Freudenstein, 2005).

though  $a'$  is a character state shared by the taxa A and C, this state does not imply that A and C share a more recent ancestor not shared by B. The situation is different when we consider the terminal taxa A, C, and D. In this case, because the character  $a'$  is an apomorphic (or derived) state present in A and C whereas D contains the plesiomorphic (or ancestral) state  $a$ , there is evidence that A and C share a more recent ancestor not shared by D.

It should be noted that the distinction between plesiomorphies and apomorphies is meaningless if we don't specify the group of biological taxa under study. In a group of two taxa, the distinction between ancestral (or plesiomorphic) and derived (or apomorphic) character states does not occur. The distinction between derived and ancestral character states requires at least three taxa. Furthermore, a character state can be derived or ancestral depending on the taxa considered. For instance, in Fig. 3, the character state  $a'$  is ancestral if we are studying the phylogeny of A, B, and C, but derived if we are studying the terminal taxa A, C, and D.

### 3.2. *Cladistics after Hennig*

Some cladists after Hennig have argued that not only is the assumption of evolution unnecessary for justifying cladistic methods, but cladistics would be better off if formulated independently of evolutionary theory (Platnick, 1979, 1982, 1985; Nelson and Platnick, 1981; Brower, 2000). In this way of understanding cladistics, systematics is supposed to provide evidence for evolution – rather than the opposite. This version of cladistics is usually referred as “pattern cladistics” – as opposed to “process cladistics” which includes Hennig and others sharing the assumption that evolution is necessary to justify cladistics.

An important motivation for pattern cladistics is the idea that the evolutionary models used to justify cladistics involve contentious claims (cf. Beatty, 1982; Platnick, 1985, p. 90). For example, Hennig subscribed to the view that dichotomous trees (i.e., each node in a tree can only give rise to two line segments) should be favored, instead of trees with more than two branches. In some passages, Hennig seems to justify this methodology by appealing to a specific speciation model, according to which speciation events only happen via splitting of an ancestral species into two new species (Hennig, 1966, pp. 207–11).<sup>12</sup> For Platnick (1979), this speciation model has

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<sup>12</sup>Hennig himself is not entirely clear about his view on this issue. For Hennig also

the following nontrivial consequences: (i) there is no speciation without splitting; and (ii) species become extinct at branching points. Both (i) and (ii) are contentious claims in evolutionary theory. (i) is inconsistent with theories of speciation in which speciation may occur: (a) via gradual change in a single lineage (or anagenesis); and (b) by hybridization. With respect to (ii), it excludes the possibility of an ancestral species surviving past a speciation event (Wiley, 1981, p. 105). According to pattern cladistics, if the methods of cladistics can be justified without appealing to a specific model of speciation, then cladistics becomes compatible with different theories about speciation. So, if pattern cladistics is adopted, then one cannot reject cladistic methods because it appeals to faulty models of evolution.

Alternatively Platnick (1979) proposes a justification for Hennig’s commitment to dichotomous trees without relying on any theory about speciation. For Platnick (1979, 1985) dichotomous trees should be favored not because of any assumption about evolution, but because dichotomous trees contain higher information content. In order to show this, Platnick (1979) considers an example of a dichotomous and a trichotomous tree for the same terminal taxa, drawn in Fig. 4. The trichotomous tree in Fig. 4a predicts that, if we take a sample of the terminal taxa, then we will find the presence of: 1. apomorphies shared by all three terminal taxa; and 2. characters unique to each terminal taxon (i.e., autapomorphies). In addition to 1. and 2., the dichotomous tree in Fig. 4b also predicts the presence of: 3. synapomorphies only shared by whipspiders and spiders.

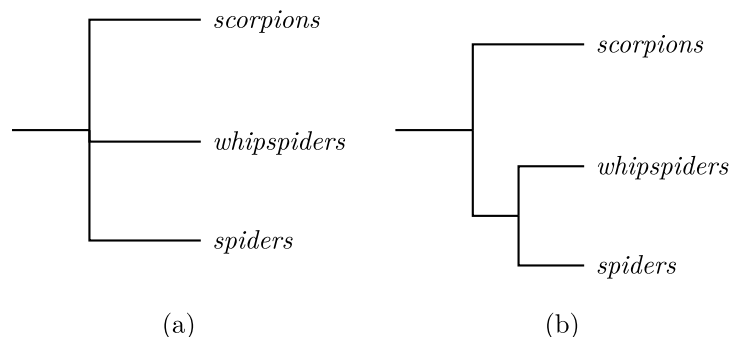
Based on this difference between the trees in Fig. 4a and Fig. 4b, Platnick argues that dichotomous trees are preferable to trichotomous trees because they allow us to test an additional hypothesis (i.e., 3.).<sup>13</sup> No specific theory of speciation is therefore necessary to justify the preference for dichotomous trees.

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suggests that the use of dichotomous trees in cladistics is just a “methodological principle” – instead of being an empirical claim. For a discussion about Hennig’s view about the principle of dichotomy, see Rieppel (2010).

<sup>13</sup>Following Popper (1968), Platnick (1979) assumes, conjectures with more empirical content (or, more falsifiable) are preferable to conjectures with less empirical content. This assumption is crucial in Platnick’s argument: if less falsifiable conjectures can be more preferable, then Platnick’s conclusion (i.e. dichotomous trees are preferable to trichotomous trees) would not follow from his argument. For a general discussion of the different uses of Popper’s views in evolutionary theory and cladistics, see Hull (1999) and Sober (1988).

Figure 4: Examples of a trichotomous (a) and dichotomous (b) tree. From Platnick (1979, p. 540).



### 3.3. Pattern cladistics and historical essences

Promoters of pattern cladistics have proposed non-evolutionary explanations for other methodological assumptions adopted by Hennig (1966), such as the *principle of parsimony* as used in cladistics. The principle of parsimony is a method of phylogenetic inference according to which, given a set of phylogenetic hypotheses about a group of taxa, we should favor the hypothesis that requires the fewest changes in character state. Brower claims that parsimony is justified not because of evolutionary reasons, but simply because the use of this principle provides “the simplest theoretical framework necessary and sufficient to account for the data” (Brower, 2000, p. 144). Brower’s view is that the principle of parsimony is a general principle in science and, accordingly, it does not require an evolutionary explanation.

Nevertheless, as opposed to pattern cladists, the process cladists follow Hennig’s lead justifying cladistic methods using evolutionary history. For instance, Ridley (1986) thinks that parsimony is justified because evolutionary change is relatively improbable.<sup>14</sup> Wiley (1979, 1981) argues that cladistic

<sup>14</sup>In more detail, Ridley’s point is that:

It is unlikely enough that all the mutations should arise and be selected for in one species, but that similar events should take place independently in another is even more improbable. Shared characters are therefore more likely to be due to common ancestry than to convergence. The eye shared by humans and chimps is less likely to be convergent than described from a common ancestor (Ridley, 1986, p. 82).

analysis should contain evolutionary information but, different from Hennig (1966), he grants that the trees obtained from cladistic analysis may exhibit trichotomous branching – e.g. the case in which a lineage is dichotomized but the ancestral species survives the speciation event (Wiley, 1981, p. 105). The question of whether evolution should rely on evolutionary theory is still a matter of ongoing debate (e.g. Kluge, 1997; Brower, 2000; Scotland, 2000; Kluge, 2001). My intention in highlighting this dispute is not to provide an answer to this question but to make the point that not every cladist appeals to genealogy when defining biological taxa.

As discussed in section 3.1, Hennig’s definition of monophyly is *genealogical*: a monophyletic group contains the common ancestor and all of its descendants. However, as discussed above, pattern cladists do not think that the branching diagrams obtained from cladistic analysis, the cladograms, are depictions of evolutionary history. Instead, cladograms are simply summaries of character distribution, devoid of any genealogical information. As an alternative to a genealogical definition of monophyly, pattern cladists hold that biological taxa should be defined in terms of characters (Baum and Donoghue, 1995). An example of a character-based definition of monophyly is provided by Farris (1974): a group is monophyletic if its group membership character appears uniquely derived and unreversed.<sup>15</sup> Thus, although both process and pattern cladistics use apomorphies to diagnose monophyletic groups, *only process cladistics defines biological taxa in terms of genealogical relations*. This contrast between process and pattern cladistics brings to the fore an important limitation of the aforementioned argument for historical essentialism; i.e., that historical essentialism is justified given how cladists define biological taxa.

Arguments that appeal to consensus of a group – like the cladistic school – are convincing only if there is evidence of such a consensus. As discussed above, an important group of cladists, the pattern cladists, define taxa in terms of characters instead of genealogy. Thus to argue for historical essentialism based on cladistics falsely assumes that cladists for the most part

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However, the view that parsimony is justified because homoplasies (shared characteristics due to independent evolution) are rare has been strongly criticized. See Sober (1988, 2004) for further details.

<sup>15</sup>Given a character with states 0 (ancestral) and 1 (derived), a group membership character is reversed when it transformed from state 1 to 0. For further details, see Platnick (1977).

define biological taxa in terms of evolutionary history. Hence, if cladistics supports historical essentialism, then additional premises must be provided: that process cladism is right and that pattern cladism is wrong.<sup>16</sup>

However, one may object, pattern cladists can define biological taxa without relying on genealogical relations, but still believe that common ancestry is an essential attribute to biological taxa. I agree that this might be the case; pattern cladists could be historical essentialists. But I think this objection misses the point of my argument. My point is not about whether pattern cladistics is *consistent* with historical essentialism; rather, my thesis is that an important form of cladism, pattern cladism, does not *justify* historical essentialism. Hence, if cladistics justifies historical essentialism, then only process cladism can perform such a role.

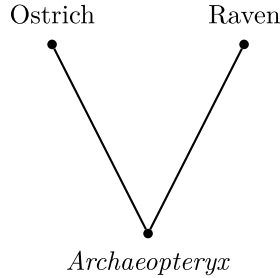
One might also object that LaPorte and Griffiths have process cladism in mind when they appeal to cladism to justify historical essentialism. For this reason, the objection continues, my point that pattern cladistics doesn't justify historical essentialism is irrelevant to the discussion about historical essences. I find this objection unsatisfactory because, even if LaPorte and Griffiths refer to process cladism in their argument (or any other version of cladism), this does not exempt them from showing why the chosen version of cladism is better off than pattern cladism when defining biological taxa – mainly when we take into consideration that pattern cladistics is a prominent view in current systematics. For their defense of historical essentialism is not presented as being conditioned upon process cladistics being correct. Nevertheless, even if historical essentialists can justify why they favor process cladistics, in the next section I argue that cladistics (be it pattern or process cladistics) provides inadequate justification for historical essentialism.

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<sup>16</sup>One potential concern with my argument of this section is that, even though historical essentialism is a view on nonactual circumstances, my argument is not premised on modal considerations. That might raise the suspicion that my argument is not properly addressing historical essentialism. However, despite the fact that the conclusion of LaPorte's and Griffiths' argument is a modal claim (i.e., biological taxa contain historical essences), not every premise in their argument is a statement about nonactual circumstances. As discussed earlier, one of the premises in their argument is an assumption about how cladists define biological taxa and that's the premise I'm targeting at in this section.



Figure 5: A tree representing the ancestor-descendant relations between *Archaeopteryx*, ostrich, and raven. From Kitching et al. (1998, p. 12).



#### 4. Argument 2: monophyly and historical essences

Suppose there is a clade, the clade Aves, containing the taxa *Archaeopteryx*, ostrich and raven, as drawn in Fig. 5. So, in the actual world, *Archaeopteryx* is the most recent ancestor of the clade Aves. According to historical essentialism, *Archaeopteryx* should be the most recent ancestor of Aves in *nonactual* worlds as well. As LaPorte states it, if *A* is the (actual) stem of Aves (i.e., a species of *Archaeopteryx*), then “The relevant clade [Aves] includes, in any possible world, all and only the organisms in and descended from species *A*” (LaPorte, 2004, p. 12). Thus, what is controversial about historical essentialism is not that *Archaeopteryx* is the most recent ancestor of Aves in the actual world (that’s taken for granted in our Aves example). Rather, the controversial bit is the claim that *Archaeopteryx* is also the most recent ancestor in nonactual worlds. The goal of this section is to assess this controversial claim.

For historical essentialists Aves has *Archaeopteryx* as its most recent ancestor in nonactual worlds because of how cladists define Aves. As discussed, cladists define biological taxa as monophyletic groups. Thereby, the argument for historical essences in Aves comprises two premises: that in the actual world, *Archaeopteryx* is the most recent ancestor of Aves; and that in every possible world that Aves exists, Aves is a monophyletic group. I shall argue that this line of reasoning is not valid. Both premises can be true and, yet, *Archaeopteryx* may not be the most recent ancestor of Aves in a nonactual world. To define Aves as a monophyletic group is not sufficient to guarantee that Aves has the same most recent ancestor in nonactual worlds as it does in the actual world.

The argument for historical essences depend on how we define “monophyly”. Like Hennig, one might define what a monophyletic group is genealogically: monophyletic groups contain a common ancestor and all of its descendants. According to this way of defining monophyletic groups, apomorphies are used as *evidence* rather than a *definition* of monophyletic groups. Alternatively, like Farris (1974), one might define monophyletic groups in terms of apomorphies (cf. Baum and Donoghue, 1995). Accordingly, there are two ways one can interpret the argument for historical essentialism depending on the definition of monophyletic groups one chooses. In what follows, I try to show that the argument for historical essences fails in both ways of defining monophyletic groups.<sup>17</sup> I begin considering the definition of monophyletic groups in terms of apomorphies.

According to the argument for historical essentialism, because Aves is a monophyletic group, the most recent common ancestor of Aves in non-actual worlds is also *Archaeopteryx*. In fact, to know that ostrich, raven and *Archaeopteryx* form a monophyletic group in a nonactual world gives us the information that they all share a more recent common ancestor in that world. However, I shall argue, because apomorphies are not sufficient to single out the most recent common ancestor, we do not know what is *the* most recent common ancestor. Accordingly, apomorphies alone cannot guarantee that Aves has *Archaeopteryx* as its most recent common ancestor in nonactual worlds. The fact that Aves shares certain apomorphies is compatible with ostrich being the most recent common ancestor, for instance. Here is my reason why I think that apomorphies do not single out *Archaeopteryx* as an ancestral taxon in nonactual worlds. In order to determine whether *Archaeopteryx* is the common ancestor of the clade by using characters, *Archaeopteryx* must have a feature not shared by the other two taxa (i.e. ostrich

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<sup>17</sup>Earlier I argued that the argument for historical essences can only take off if process cladistics is right and pattern cladistics is wrong. Based on that, one might object that once we embrace process cladistics then there is no motivation for defining monophyletic groups in terms of characters. For this reason, the objection continues, the only way historical essentialists can define monophyletic groups is in terms of genealogy – which makes the definition of monophyly in terms of characters irrelevant to my argument. However, considering both ways of defining monophyletic groups is relevant because that makes my two arguments against historical essentialism independent from each other. That leaves room for someone to find my first argument unconvincing but, still, accept the argument from this section.

and raven).<sup>18</sup> Thus there are two ways a historical essentialist might try to argue that *Archaeopteryx* is the common ancestor of the clade Aves by utilizing apomorphies: (I) there is a synapomorphy shared by ostrich + raven but absent in *Archaeopteryx*; and (II) *Archaeopteryx* contains an autapomorphy, a character not shared by the group ostrich + raven. However, neither (I) nor (II) provide evidence for the claim that *Archaeopteryx* is the common ancestor of the clade.

Concerning (I), ostrich + raven contain the synapomorphy of having a pygostyle (the bone where the tail feathers attach) not shared by *Archaeopteryx*. Nevertheless, there are many animals that do not have a pygostyle such as humans. The property of not having a pygostyle then fails to show that *Archaeopteryx* is the common ancestor of the clade. Regarding (II), even if *Archaeopteryx* possesses an autapomorphy, this does not imply that *Archaeopteryx* is the ancestral group of the clade. For there is no connection between possessing an autapomorphy and appearing earlier in time. For instance, the autapomorphies unique to *Homo sapiens* do not make humans the ancestral species of other taxa in the Hominidae. Therefore, even though apomorphies provide membership conditions for a monophyletic group, they do not distinguish which taxon is the most recent ancestor of the clade.<sup>19</sup>

Now consider the definition of monophyletic groups in terms of genealogy (i.e., monophyletic groups contain a common ancestor and all of its descendants). Once again, the historical essentialist faces the same problem: the assumption that Aves is a clade in every possible world it exists tells us that the members of Aves all descend from *a* common ancestor without specifying which taxon is *the* most recent common ancestor. Aves can be a clade and, yet, *Archaeopteryx* in particular may not be most recent ancestor of Aves. In order to show why that's the case, I'd like to introduce the distinction between *cladograms* and *phylogenetic trees*.

Cladograms are used to represent hypotheses about monophyletic groups; and cladograms display taxa at their tips only. Phylogenetic trees are representations of ancestor-descendant relationships and their internal nodes stand for biological taxa. For instance, the cladogram in Fig. 6 tells us that the

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<sup>18</sup>The following discussion is based on Kitching et al. (1998, pp. 12-14) comments about the clade depicted in Fig. 5.

<sup>19</sup>For further references about the impossibility of using apomorphies to identify ancestral taxa see: Engelmann and Wiley (1977), Wiley (1981, pp. 105-107), Kitching et al. (1998, pp. 13-14), and Schuh (2000, pp. 84-86).

Figure 6: A cladogram expressing the relation among the taxa A, B, and C.

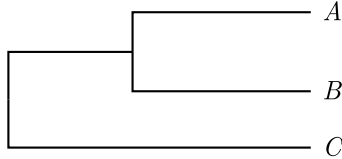
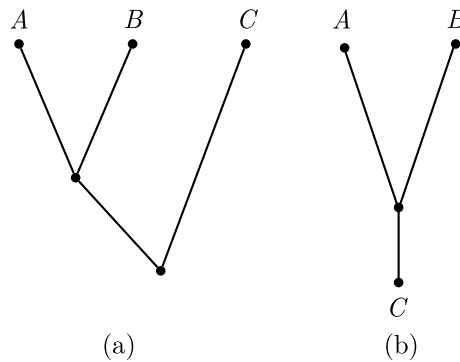


Figure 7: Phylogenetic trees expressing different ancestor-descendant relationships among the taxa A, B, and C. From Sober (1988, p. 23).



taxa A and B belong to a clade that does not contain C. However, different ancestor-descendant relationships are consistent with the cladogram in Fig 6. Some of these ancestor-descendant relationships are depicted by the phylogenetic trees in Fig. 7. According to Fig. 7a, the common ancestor of A and B is not an ancestor of C; in Fig. 7b, C is an ancestor for both A and B. Even though these two phylogenetic trees represent different ancestor-descendant relations, they are both compatible with the cladogram in Fig 6.<sup>20</sup>

A way of describing the difference in information content between cladograms and phylogenetic trees is via the contrast between *sister-group* and *ancestor-descendant* relations. To establish that *Archaeopteryx* belongs to a clade containing ostrich + raven only shows that *Archaeopteryx* shares a more

<sup>20</sup>For further details about the relation between cladograms and phylogenetic trees, see Sober (1988), pp. 21–25.

recent ancestor with the group ostrich + raven than to a third group.<sup>21</sup> Otherwise stated, *Archaeopteryx* and ostrich + raven are sister-groups. Nothing is said about whether *Archaeopteryx* is the common ancestor of the remaining taxa of the clade. The idea here is that the sister-group relation is collateral, not ancestral-descendant (Hull, 2001, pp. 223-24). Thus, instead of specifying ancestral-descendant relations, cladograms only supply sister-group relations.

The difference between cladograms and phylogenetic trees is important for us because hypotheses about monophyletic groups give us cladograms, not phylogenetic trees. But, as discussed above, cladograms don't specify which taxon *in particular* is the most recent ancestor of Aves. From a cladogram representing the clade Aves, we cannot extract the information that *Archaeopteryx* is the most recent ancestor of Aves. In contrast, historical essences specify what is *the* most recent ancestor of Aves. Hence, to understand monophyly in genealogical terms does not vindicate the existence of historical essences. Moreover, as I argued previously, we get an analogous result if we consider the set of apomorphies the members of Aves share. Apomorphies alone do not contain any information about which taxon is the common ancestor of Aves. So, no matter if monophyletic groups are defined in terms of characters or in term of genealogy, Aves can be monophyletic groups in every possible world without possessing historical essences.

## 5. Final considerations

Briefly, these are the main ideas discussed in this paper so far. In Griffiths (1999) and LaPorte (2004) we find the claim that cladism supports historical essentialism. Given that cladistics is the dominant school in taxonomy, this seems to be a powerful argument for historical essentialism. In this paper, however, I presented two reasons showing why cladistics does not justify historical essentialism: (1) arguments that appeal to a consensus of experts are convincing only if such a consensus in fact exists. I argued that the consensus necessary to warrant historical essentialism among cladists is absent (sec. 3); (2) cladistic definitions do not specify which taxon is the most recent ancestor of a clade; so such methods do not provide sufficient evidence for historical essentialism (sec. 4). If sound, these two arguments show that

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<sup>21</sup>As observed by Sober, "Judgments of monophyly are *contrastive*: two items belong to a monophyletic group only in contrast to a third one that does not" (Sober, 1988, p. 19).

historical essentialism, as proposed by Griffiths (1999) and LaPorte (2004), is unjustified.

The goal of this paper was to show that a *particular* argument for historical essentialism is unsatisfactory. This paper is thus consistent with the possibility of an alternative argument for historical essentialism – as well as for other versions of biological essentialism.<sup>22</sup> Hence, this paper leaves a few questions unanswered. Is it possible to have an alternative argument for historical essentialism (or any other version of essentialism)? If biological essentialism is unsatisfactory, what are the alternatives? Rather than providing a definite answer to these questions, I explore below some potential ramifications of this paper for the general debate concerning biological essentialism. I begin with the suggestion that some of the difficulties with LaPorte’s and Griffiths’ essentialism might also apply to other versions of biological essentialism.

One of the themes of my paper was that biological practice doesn’t provide a ready-made definition of biological taxa that we could use in all contexts. I illustrated this point by citing the disagreement between process and pattern cladistics.<sup>23</sup> Since there isn’t a ready-made biological definition, an argument for essentialism will have to choose among such definitions (as LaPorte and Griffiths did). But, in doing so, essentialists will face the challenge of justifying which choice they make. In my first argument, I argued that such a justification is lacking in LaPorte’s and Griffiths’ argument. They don’t provide reasons for favoring process cladistics to pattern cladistics. Thereby, rather than being an isolated difficulty of LaPorte’s and Griffiths’ essentialism, any attempt of employing biological practice to back up biological essentialism might run into similar difficulties.

Even after choosing a particular definition, applying such a definition in modal contexts poses challenges. In particular, consider once again the definition of “Mammalia” according to de Queiroz: “the clade stemming from the most recent common ancestor of horses and echidnas” (de Queiroz, 1995, p. 224). This definition by itself does not tell what has to be the same for a taxon to be Mammalia in a nonactual world. De Queiroz favored the view that Mammalia has to have the same specifiers (i.e., echidnas and horses)

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<sup>22</sup>For a recent discussion of the modern versions of biological essentialism, see Ereshefsky (2010b).

<sup>23</sup>Within cladistics, disagreements over the PhyloCode would be another example.

in every possible circumstance – which led to Ghiselin’s objection (Sec. 2). Unlike de Queiroz, LaPorte thinks that it’s the most recent ancestor (not the specifiers) that is necessarily the same. However, these decisions were not licensed by the definition of “Mammalia” itself. So given a definition of a taxon (e.g., de Queiroz’ definition of Mammalia), there might be different ways we can interpret this definition in modal contexts (e.g., de Queiroz’ and LaPorte’s ways). Also, when we use notions such as “ancestor” and “specifiers” in modal contexts, there is the problem of specifying the identity conditions of these notions across possible worlds. For instance, one of the attractive features of historical essentialism is that it provides an alternative to intrinsic essentialism, the view that biological essences are intrinsic properties. However, if the identity conditions of *Archaeopteryx* across possible worlds require intrinsic properties, then such hybrid historical essentialism might be committed to the view that biological essences are partially intrinsic.<sup>24</sup> But if that’s the case, arguments against intrinsic essentialism could apply to hybrid historical essentialism as well. In sum, as the debate about historical essences illustrates, definitions of biological taxa generally are not designed to apply to modal contexts out of the box. Thus, citing biological practice is insufficient to warrant essentialism not simply because there isn’t a consensus about how to define biological taxa, but also because biological definitions alone generally don’t provide guidelines as to how we should apply them in modal contexts.

Despite the difficulties biological essentialism might face, to simply state that essentialism is false seems to leave us in an unsettling position. As discussed in the introduction, LaPorte and Griffiths claim that essences help us explain shared features among members of the same taxon. But if LaPorte and Griffiths are correct in this regard, then a nonessentialist route would leave us with unanswered questions that essentialism was designed to solve. Possibly, the difficulties with essentialism simply indicate how we can improve our essentialist theories rather than showing that we have to reject essentialism altogether. However, it’s worth noting, recent work in philosophy biology has suggested that biological essentialism has no explanatory import (e.g., Okasha, 2002) and also that we can explain similarities among members of the taxon without postulating essences (e.g., Ereshefsky, 2010b).

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<sup>24</sup>Incidentally, Devitt (2008) has recently argued for a version of essentialism according to which essences are partly intrinsic.

In sum, on one hand it's not clear how biological practice can warrant biological essentialism: biological practice does not give us a single answer as to how we should define biological taxa, and the use of biological definition in modal contexts introduces new challenges. On the other hand, a viable nonessentialist alternative must show how we can account for the explanatory role of biological taxa without relying on essences.

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## References

- Baum, D., Donoghue, M., 1995. Choosing among alternative 'phylogenetic' species concepts. *Systematic Biology* 20, 560–73.
- Beatty, J., 1982. Classes and cladistics. *Systematic Zoology* 31, 25–34.
- Brower, A., 2000. Evolution is not a necessary assumption of cladistics. *Cladistics* 16, 143–54.
- de Queiroz, K., 1992. Phylogenetic definitions and taxonomic philosophy. *Biology and Philosophy* 7, 295–313.
- de Queiroz, K., 1995. The definitions of species and clade names: a reply to Ghiselin. *Biology and Philosophy* 10, 223–28.
- Devitt, M., 2008. Resurrecting biological essentialism. *Philosophy of Science* 75, 344–382.
- Engelmann, G., Wiley, E., 1977. The place of ancestor-descendant relationships in phylogeny reconstruction. *Systematic Zoology* 26, 1–11.
- Ereshefsky, M., 2001. *The poverty of the Linnaean hierarchy: a philosophical study of biological taxonomy*. Cambridge University Press, Cambridge.
- Ereshefsky, M., 2010a. Species. In: Zalta, E. N. (Ed.), *The Stanford Encyclopedia of Philosophy*, spring 2010 Edition. <http://plato.stanford.edu/archives/spr2010/entries/species/>.



- Ereshefsky, M., 2010b. What's wrong with the new biological essentialism. *Philosophy of Science* 77, 674–685.
- Farris, J., 1974. Formal definitions of paraphyly and polyphyly. *Systematic Zoology* 23, 548–554.
- Freudenstein, J., 2005. Character, states, and homology. *Systematic Biology* 54, 965–73.
- Ghiselin, M., 1974. A radical solution to the species problem. *Systematic Zoology* 23, 536–44.
- Ghiselin, M., 1995. Ostensive definitions of the names of species and clades. *Biology and Philosophy* 10, 219–222.
- Griffiths, P., 1996. Darwinism, process structuralism, and natural kinds. *Philosophy of Science* 63, S1–S9.
- Griffiths, P., 1999. Squaring the circle: natural kinds with historical essences. In: Wilson, R. A. (Ed.), *Species: new interdisciplinary essays*. MIT Press, Cambridge, pp. 208–228.
- Hennig, W., 1966. *Phylogenetic Systematics*. University of Illinois Press, Chicago.
- Hull, D., 1978. A matter of individuality. *Philosophy of Science* 45, 335–360.
- Hull, D., 1999. The use and abuse of sir Karl Popper. *Biology and Philosophy* 14, 481–504.
- Hull, D., 2001. The role of theories in biological systematics. *Studies in History and Philosophy of Biological and Biomedical Sciences* 32, 221–38.
- Kitching, I. J., Forey, P. L., Humphries, C. J., Williams, D. M., 1998. *Cladistics: the theory and practice of parsimony analysis*. Oxford University Press, Oxford.
- Kluge, A., 1997. Testability and the refutation and corroboration of cladistic hypotheses. *Cladistics* 13, 81–96.
- Kluge, A., 2001. Parsimony with and without scientific justification. *Cladistics* 17, 199–210.

- Kripke, S., 1980. *Naming and Necessity*. Harvard University Press, Cambridge.
- LaPorte, J., 2004. *Natural kinds and conceptual change*. Cambridge University Press, Cambridge.
- Mayr, E., 1969. *Principles of Systematic Zoology*. Harvard University Press, Cambridge.
- Mellor, D., 1977. Natural kinds. *British Journal for the Philosophy of Science* 28, 299–312.
- Nelson, G., Platnick, N., 1981. *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.
- Nixon, K., Carpenter, J., 2000. On the other ‘phylogenetic systematics’. *Cladistics* 16, 298–318.
- Okasha, S., 2002. Darwinian metaphysics: species and the question of essentialism. *Synthese* 131, 191–213.
- Platnick, N., 1977. Paraphyletic and polyphyletic groups. *Cladistics* 26, 195–200.
- Platnick, N., 1979. Philosophy and the transformation of cladistics. *Systematic Zoology* 28, 537–46.
- Platnick, N., 1982. Defining characters and evolutionary groups. *Systematic Zoology* 31, 282–84.
- Platnick, N., 1985. Philosophy and the transformation of cladistics revisited. *Cladistics* 1, 87–94.
- Popper, K., 1968. *The Logic of Scientific Discovery*. Harper and Row, New York.
- Putnam, H., 1975. Is semantics possible? In: *Mind, Language, and Reality: Philosophical Papers*. Vol. 2. Cambridge University Press, Cambridge, pp. 139–52.
- Ridley, M., 1986. *Evolution and classification: the reformation of cladism*. Longman, London.

- Rieppel, O., 2010. Willi Hening's dichotomization of nature. *Cladistics* 26, 1–10.
- Schuh, R., 2000. *Biological systematics: principles and applications*. Comstock Publishing, New York.
- Scotland, R., 2000. Taxic homology and three-taxon statement analysis. *Systematic Biology* 49, 480–500.
- Sereno, P., 2005. The logical basis of phylogenetic taxonomy. *Systematic Biology* 54, 595–619.
- Sober, E., 1988. *Reconstructing the past: parsimony, evolution, and inference*. MIT Press, Cambridge.
- Sober, E., 2004. The contest between parsimony and likelihood. *Systematic biology* 53, 644–653.
- Sokal, R., Sneath, P., 1963. *The Principles of Numerical Taxonomy*. W. H. Freeman, San Francisco.
- Stevens, P., 1991. Character states, morphological variation, and phylogenetic analysis: a review. *Systematic Botany* 16, 553–83.
- Thiele, K., 1993. The holy grail of the perfect character: the cladistic treatment of morphometric data. *Cladistics* 9, 275–304.
- Wiley, E., 1979. Cladograms and phylogenetic trees. *Systematic Zoology* 28, 88–92.
- Wiley, E., 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. John Wiley & Sons, New York.
- Wilson, R., Barker, M., Brigandt, I., 2007. When traditional essentialism fails: biological natural kinds. *Philosophical Topics* 35, 189–215.