Taxa hold little information about organisms: Some inferential problems in biological systematics

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Abstract   The taxa that appear in biological classifications are commonly seen as representing information about the traits of their member organisms. This paper examines in what way taxa feature in the storage and retrieval of such information. I will argue that taxa do not actually store much information about the traits of their member organisms. Rather, I want to suggest, taxa should be understood as functioning to localize organisms in the genealogical network of life on Earth. Taxa store information about where organisms are localized in the network, which is important background information when it comes to establishing knowledge about organismal traits, but it is not *itself* information about these traits. The view of species and higher taxa that is proposed here follows from examining three problems that occur in contemporary biological systematics and are discussed here: the problem of generalization over taxa, the problem of phylogenetic inference, and the problematic nature of the Tree of Life.

Keywords   Inference · Phylogenetic inference · Species · Systematic biology · Tree of Life

1 Introduction

The taxa that appear in biological classifications, such as species, genera, families, and so on, are commonly seen as representing information about their member organisms. Knowing what species a given organism belongs to seems to

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enable us to reliably infer a host of its properties. If I know that the animal I am looking at is an *Ornithorhynchus anatinus*, I know without examining it more closely that it lactates to feed its offspring, that it lays eggs, that is has a venomous spur on its hind extremities, that its natural habitat consists of rivers, streams and lagoons in eastern Australia and Tasmania, that it eats mainly aquatic invertebrates and small fish, that it has electroreceptors in its bill, that it has webbed feet, and so on. In general, knowledge about the kind of organism one is considering seems to constitute a solid basis for inferences regarding what it will look like and how it will behave under particular circumstances. The same holds to a lesser extent for an organism's membership in higher taxa. When we know what genus, family, order, etc. an organism belongs to, this tells us something about the properties it can be expected to exhibit, even though higher taxa membership generally conveys less information about organisms than their membership in lower taxa.

This is, among other things, why biological systematics and classification are such important parts of the life sciences: they order biological diversity into a hierarchically structured system of groups that provides researchers with a storage system of knowledge about the organisms they work with. As Mayr and Bock put it:

> Information storage and retrieval is a major objective of most ordering systems. In such systems, objects are grouped together (on the basis of various criteria) that permit storage and retrieval of information about these objects. Classifications, therefore, can serve as summaries of a great deal of information (Mayr and Bock 2002: 171–172).

As such "summaries of information", classifications and the groups that feature in them serve as the backbone of biological research, and it is hard to imagine scientific research being possible at all without them. And in the public sphere, too, taxa feature as information storage units—consider how classifications of microorganisms are used in medical practice, how taxon membership specifications feature in cooking (think of the importance of correctly identifying mushrooms before eating them), in gardening, in woodworking (where one needs to know the properties of the wood when using it for a particular purpose), in nature management, in zoos and natural history museums, and in many more contexts.

While taxa thus seem to serve successfully as information storage units, in this paper I want to go beyond appearances and examine in what way, exactly, taxa function in the context of the storage and retrieval of biological information. Note that the term 'information' is used here in a non-technical sense: the kind of information under consideration is knowledge about intrinsic or extrinsic properties of organisms (in the sense of Mayr and Bock 2002, quoted above), not information in the sense of the debate on genetic information in the philosophy of biology (e.g., Maynard Smith 2000; Griffiths 2001; Sarkar 2003; Stegmann 2009). That is, I am concerned with investigators using the taxon membership of organisms to obtain information about organismal traits, rather than with information that would be stored in a taxon's member organisms. I will argue that

taxa do not actually store much information of the former sort about their member organisms (even though they do store *some* information). Rather, I want to suggest, taxa should be understood as functioning to localize organisms in the genealogical network of life on Earth. Taxa store information about where organisms are localized in the network—and this is important background information when it comes to establishing knowledge about organismal traits, but it is not *itself* information about these traits.

The view of species and higher taxa that is proposed here follows from examining three problems that occur in contemporary biological systematics: the problem of generalization over taxa (Sect. 3), the problem(s) of phylogenetic inference (Sect. 4), and the problematic nature of the Tree of Life (Sect. 5). The first problem pertains to the quality of the information often associated with taxa, the second to the nature of the presumed information carriers (taxa), and the third to the embedding of taxa in a hierarchical structure. These problems add to each other and constitute a cumulative challenge to the view that taxa contain information about their member organisms' traits. Before addressing these issues, Sect. 2 explicates the reasons for thinking that taxa function as information storage units. Section 6 presents a suggestion as to how, notwithstanding the aforementioned problems, taxa can still play an important epistemic role in biological reasoning as providers of background information. Section 7 concludes.

2 Taxa as information storage units

The inferences that we make in practice about the morphological, genetic and behavioral traits of organisms on the basis of their species membership have a tendency to turn out well. If you have seen one platypus, it seems, you have seen them all, even though individual platypuses of course vary in size, weight, health aspects, and so on. Similarly, inferences over higher taxa usually seem reliable, even though inferential reliability generally declines with higher taxon rank.[1] Knowing that a particular organism is a member of the class Insecta tells us less about its traits than knowing that it is a member of the order Odonata, which in turn tells us less than knowing that it is a member of the genus *Libellula*. Still, for higher taxa, too, taxon membership conveys *some* information about the organisms of the taxon. In his influential paper on causation in biology, Mayr put it thus:

> (…) If I have identified a fruit fly as an individual of *Drosophila melanogaster* on the basis of bristle pattern and the proportions of face and eye, I can 'predict' numerous structural and behavioral characteristics which I will find if I study other aspects of this individual. If I find a new species with the diagnos-

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[1] The decline of inferential reliability with increase in taxon rank is due to the inclusivity of taxa: higher taxa simply encompass larger parts of biodiversity than lower taxa. There is no strict correlation between the degree to which reliable inferences are possible over a taxon and the taxon's rank, though.

tic key characters of the genus *Drosophila*, I can at once "predict" a whole set of biological properties (Mayr 1961: 1504–1505).

Note that the inference that Mayr makes in the first part of the quotation is based on a generalization over the members of the species. The prediction that the particular fruit fly under consideration will exhibit properties p_1, p_2, p_3, etc. crucially rests on observations of the presence of properties p_1, p_2, p_3, etc. in a sample of the species' members. In other words, I can infer "numerous structural and behavioral characteristics" of the fruit fly under consideration only if these have already been observed to be present in a number of other members of the same species *and* there is a basis for generalizing these observations to all members of the species (i.e., there are good reasons to assume that members of a species generally tend to exhibit very similar properties). The same holds for the inference that is made in the second part of the quotation: I can infer what properties are likely present in the members of the newly discovered *Drosophila* species if there are observations about the properties that are typically found in other *Drosophila* species *and* there is a basis for generalizing from the known to the unknown species.

What is the basis for generalizing in these cases? The reason for the predictive power of species membership, Mayr suggested, lies in the biological basis of taxa, namely common descent. Taxon membership, Mayr pointed out, doesn't merely tell us *what* traits an organisms can be expected to exhibit, but also *why*. The knowledge that an organism is a *Drosophila melanogaster* implies that it has a particular set of properties *because* it is descended from a long line of organisms that also exhibit this set of properties. This is similar for higher taxa, albeit for much smaller sets of traits. The knowledge that a particular organism is a member of the subphylum Vertebrata does not only imply that (if it doesn't have a severe developmental disorder) it is very likely to have a backbone, but also that it is likely to have a backbone *because* it is descended from a distant ancestral population in which this trait first evolved.

This dual role of taxa as both specifying which traits their members are likely to exhibit and why they are likely to do so, prompted Mayr to argue that biological classifications are not only ordering systems without which research would not be possible but also feature as theories in scientific research. As he put it:

> Every biological classification is a scientific theory. Classifications have the same properties as all theories in science. A given classification is explanatory, by asserting that a group of organisms grouped together consists of descendants of a common ancestor. A good classification, like a good scientific theory, has a high predictive power with respect to the assignment of newly discovered species and the pattern of variation of previously unused characters. […] Like all theories, classifications are provisional and may have to be modified in the light of new discoveries. (Mayr 1968: 546).

To be sure, the claim that biological classifications have the same properties as all scientific theories is much too strong and, moreover, left unargued by Mayr. Moreover, even if it were unproblematic, the claim that therefore every biological classification *is* a scientific theory is a *non sequitur*. Still, Mayr seems right that the

explanatory power of classifications and the taxa featuring in them points to a theoretical role for taxa that goes beyond the role of merely being information storage units. Accounts of scientific explanation often connect the capacity to explain phenomena directly or indirectly to theories. On the Covering Law account, for example, "[t]he explanation of a phenomenon […] consists in its subsumption under laws or under a theory" (Hempel and Oppenheim 1948: 152). For Hempel and Oppenheim, laws are theories (but not vice versa; Hempel and Oppenheim 1948: 159), such that subsumption under a law just is subsumption under a theory. On Kitcher's unificatory account (which he develops from the Covering Law account), too, explanations consist in showing how phenomena fit under scientific theories and in this way unifying them with the other phenomena that are covered by the same theory (Kitcher 1981). On such accounts, explaining why an organism exhibits certain traits can consist in the subsumption of this explanandum under a classification. While this does not imply that classifications *are* theories in any strict sense of the term, at the very least it does seem that classifications can perform an epistemic role—explanation—that usually is performed by scientific theories.[2] The classification of organisms into species and higher taxa is supposed to trace an important part of the causal nexus underlying similarities between organisms, thus enabling taxa to play an explanatory role.

Note how in this respect the explanatory role of taxa is the same as that of natural kinds as these are traditionally conceived. On the traditional view, every natural kind is associated with a unique set of essential properties that is exhibited by all and only the members of the kind and that causes the presence of the observable properties characteristic of members of the kind. Because of this causal relation between the essential and observable properties, kind membership explains an entities' observable properties. Although it is no longer widely held that species and higher taxa are natural kinds in this traditional sense and the debate on natural kinds has also moved beyond the traditional view towards more adequate views, the traditional idea is still present in both contexts. Many contemporary accounts retain the idea of natural kinds as groups of highly similar entities, where similarity is explained by causal factors in nature, such as causal homeostatic mechanisms or nodes in causal networks (e.g., Boyd 1999; Khalidi 2018). Often, such accounts count biological taxa among natural kinds.[3] Similarly, Mayr's view is representative for the widely held view that taxa unify organisms according to common descent that causes the presence of many traits in their member organisms (often in contrast to the absence in the members of other taxa). In this way, generalizations over taxa seem to be causally supported and therefore stable and reliable.

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[2] Recently, Leonelli (2013) also argued that some classifications in biology can be a form of theory, highlighting the explanatory role of some types of classification. However, Leonelli focused on bio-ontologies and classifications of developmental stages and not on classifications involving taxa. In this paper, I will not address the general question whether classifications can be thought of as theories but I will shed doubt on the explanatory role of the classification of organisms into taxa and thus on its status as theory.

[3] Even though I am critical of these accounts and of their counting biological taxa as natural kinds, I will not pursue the topic of natural kinds in this paper.

The preceding discussion suggests that taxa have a strong basis for their role as information storage units in the biological sciences. In the following three sections, however, I want to highlight three problems that cast doubt on this suggestion.

3 The problem of generalization

The first problem concerns the epistemic role of taxa as the bases for generalized statements. Although most generalizations over taxa that we make in practice indeed seem unproblematic, matters are not as straightforward as they are often thought to be. The problem is that the inferential basis in statements such as "Because X is a member of *Ornithorhynchus anatinus*, it is likely to exhibit properties p_1, p_2, p_3, etc." is not unequivocally determined and often does not seem to be the species at all. A number of issues must be highlighted in this regard.

First, note that none of the inferences about members of the species *Ornithorhynchus anatinus* mentioned in the previous section hold necessarily—in contrast to what we would expect of causally supported inferences over natural kinds, exceptions are the rule. Some inferences (such as the inference regarding the animal's favorite food, its webbed feet, and its ability for electroreception) are very likely to be correct, but can still turn out incorrect in some cases, which would probably be seen as noteworthy cases of developmental malfunctions. Others (such as the inference that it has a venomous spur, and the inference that it lays eggs) only hold with a chance of about 50%, assuming I don't know whether the animal that I'm looking at is a male or a female platypus.[4] And for still others there might be deeper questions regarding their correctness: when the animal in question was born in my local zoo, has lived there all of its life, and will die there too without ever having visited eastern Australia or Tasmania, what exactly does it mean to say that *this* particular animal's natural habitat is eastern Australia or Tasmania rather than my local zoo? It is one thing to say that members of the species *Ornithorhynchus anatinus* typically occur in eastern Australia and Tasmania (which is a claim about the lineage rather than about individual organisms), but it is a different thing to make a specific claim about the presumed natural habitat of one particular organism on the basis of its species membership. While the former claim is correct, the latter claim does not even seem to make sense when conceived of as a counterfactual.[5] These examples show that—while reliable generalizations can be made in this case—it is questionable whether the group referred to by the name *Ornithorhynchus anatinus* actually is the group that functions as the basis for these generalizations.

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[4] This means that the inference bases are the groups of male and female platypuses, respectively, rather than the group denoted by the name *Ornithorhynchus anatinus*.

[5] The counterfactual is "Had the animal that I'm looking at now (in my local zoo) been born in the wild, it would have lived in eastern Australia or Tasmania." I'm not sure how this claim could be true or false for the animal under consideration. While *Ornithorhynchus anatinus* is an indigenous species of eastern Australia or Tasmania, there is no reason why organisms of the species cannot be born in the wild elsewhere, for example as offspring of a pair that was shipped to a different continent and let loose in the wild.

This matter can be deepened when looking at the temporal extension of the generalizations that we usually make over species and higher taxa. As inferences of the sort discussed here are based on common descent (that is, their causal support is historical), inferences must be seen as reaching over multiple generations and thus as extended through time (implying a view of taxa as spatiotemporally extended parts of the Tree of Life). In many cases, generalizations begin with observations of the traits of contemporary or very recent members of a taxon (currently living organisms, specimen stored in natural history museums and herbaria, and perhaps drawings of a few centuries ago). The inferences that are made in most cases apply to currently living organisms and organisms of nearby past and future generations. The temporal extent of such generalizations thus typically is a small timeslice of evolutionary history. In cases in which fossil evidence is available as a basis for inferences about past organisms, the temporal extension of the inferences is larger. In any case, by being temporally extended, inferences reach over segments of the Tree of Life rather than over populations of currently living organisms.

But are the segments over which generalizations reach the taxa that are delimited and named by biologists? To achieve more clarity about the issue, let me consider how species and higher taxa are embedded in phylogenetic trees. I have discussed this elsewhere in detail (Reydon 2006) and so will be brief here. While it is widely accepted that species and higher taxa are segments of the Tree of Life, there is ongoing discussion on the question how taxa are best delimited in the tree. There are at least three different, mutually incompatible ways of delimiting species in a genealogical tree (Reydon 2006: 234–237). The choice between these options in part rests on methodological assumptions regarding phylogeny reconstruction, as well as assumptions about how evolutionary processes take place. The ongoing debates among systematists have shown that none of the options can be singled out as *the* correct way to delimit taxa in a tree—rather, depending on the assumptions in one's research program, different options are better suited than others. Thus, the boundaries of taxa in the Tree are not completely determined by nature, but also in part by researchers' choices. This makes it difficult to uphold that generalizations reach exactly over species or higher taxa—that is, that generalizations such as the ones mentioned above about platypuses or fruit flies reach *exactly* over all members of *Ornithorhynchus anatinus* and *Drosophila melanogaster*, respectively, and stay within the boundaries of these species. Why would they, if the boundaries of taxa are not given by nature?

To see the deeper roots of this issue, consider the causal basis for such generalizations. As Mayr pointed out, common descent underlies similarity among organisms of the same taxon and thus is the main factor that supports generalizations. Often, this phenomenon is denoted by the term 'phylogenetic inertia':

[P]hylogenetic inertia is what licenses induction and explanation of a wide range of properties—morphological, physiological, and behavioral—using kinds defined purely by common ancestry. If we observe a property in an organism, we are more likely to see it again in related organisms than in unrelated organisms (Griffiths 1999: 220)

Phylogenetic inertia here refers to the phenomenon that organismal traits tend to stay largely the same over longer periods of time, generation after generation. Evolution proceeds gradually and slowly, and traits are (metaphorically speaking) somewhat inert when it comes to evolutionary change. This inertia often manifests itself as a lack of optimality (Gould and Lewontin 1979: 594). Because of this inertia, we can predict that members of later generations will have largely similar traits as those of preceding generations in the same lineage.

However, all organisms throughout the tree are related by descent, no matter how similar or dissimilar they are. In addition, more closely related organisms tend to be more similar than more distantly related organisms, making reference to common descent as such inadequate as a causal explanation of similarity. In order to understand phylogenetic inertia, descent is better understood as itself encompassing a manifold of causal factors that contribute to the tendency of offspring to resemble their parents. These factors include (but are not limited to) the copying process of the genome in cell division (which itself can be analyzed as consisting of a number of processes involving a number of causes), developmental and generative entrenchment (Wimsatt 2007: Chapter 7, 2015: 369; cf. Gould and Lewontin 1979: 594), and environmental stability (i.e., offspring growing up in the same environment as their parents). Elsewhere (Reydon 2006: 244ff.), I have argued that phylogenetic inertia is due to two main causes: while some instances of phylogenetic are mainly due to stabilizing selection as an external factor, others are mainly due to developmental factors internal to the organism. Both causes can be further analyzed into a manifold of other causal factors that play a role in the conservation of traits in ancestor–descendant lineages. Regardless of how the causality underlying phylogenetic inertia is analyzed, however, the main point for the present discussion is that "the time periods over which instances of phylogenetic inertia occur do not normally coincide with the temporal extent of those basic tree-segments that biologists recognize as species" (Reydon 2006: 246).

Consider developmental factors. When the conservation of a trait is supported by factors internal to the organisms, traits will often be conserved over longer periods of time, extending across multiple species. Depending on how deeply entrenched a trait is, trait conservation can encompass a large number of lower taxa (the example of Vertebrata, mentioned above, is a case in point). Instances of stabilizing selection, in contrast, often occur over only a limited time period that is shorter than the temporal extension of the species (sometimes even only extending over a few generations). Depending on the cause underlying the conservation of a trait, thus, traits will be conserved either within only a small part of the lineage that is counted as a species or higher taxon, or for time periods far extending the lifetime of such lineages.[6] Moreover, in both cases trait conservation across splits in the tree is common and there is no reason to assume that the temporal extension of trait conservation will generally correspond to the temporal extension of species or other taxa. This means that the generalizations mentioned in Sect. 1 are not generalizations that reach over the temporal extent of the species *Ornithorhynchus anatinus*. For platypuses that

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[6] For examples and discussion, see Reydon (2006).

will exist in the near future and those that have existed in the near past, the generalizations will be reliable, but the further into the past or the future one attempts to generalize, the less reliable the inferences for many traits will be. The relevant time-scales differ between traits, as some traits are more deeply entrenched than others, and the stability of inferences also depending on contingent factors (e.g., the stability of the environment and which mutations occur at which time).

The problem of generalization over taxa, then, is that for many—if not most—generalizations the group of organisms for which the generalizations holds is not exactly or even largely coextensive with the group of members of a taxon, such that the taxon cannot be seen as the epistemic basis for the generalization. While Mayr was right to say that it is possible to predict many traits of a fruit fly when it has been identified as a member of *Drosophila melanogaster*, membership of this species *itself* is not what underwrites inferences about the properties of the organism in question. Rather, I will suggest that taxon membership functions as a placeholder for the organism's location in the genealogical nexus, allowing us to put the organism in closer or more distant relations to other organisms and in this way indirectly supporting generalizations from the traits of neighboring organisms to the organism in question. Before exploring this suggestion in Sect. 6, I will continue my examination of the problematic nature of taxa as information storage units.

4 The problem of phylogenetic inference

The conclusion from the preceding section is that inferences in which the names of species and higher taxa feature—"X is a member of *Drosophila melanogaster* and thus is likely to exhibit properties p_1, p_2, p_3, etc."—are not generalizations that extend over, or are based on, the taxon that is being referred to. Generalizations of this sort either hold only for limited parts of taxa, or extend over much larger parts of the tree, transgressing the boundaries of taxa. These problems are intensified by the problem (or rather, problem set) of phylogenetic inference (Hecht and Edwards 1977; Felsenstein 1988; 2004; Sober 1988: 1–36; Haber 2009; Velasco 2013).

Core parts of biological systematics encompass the construction ("erecting") of taxa, i.e., the placing of organisms into groups, attributing taxonomic ranks to these groups, and placing them into the context of phylogenetic history by placing them into tree-like structures that can serve as systems of classification. This is an information-intensive process in which large quantities of data on organismal traits are used to individuate taxa and to position them with respect to each other in the system. Recent decades have seen an enormous increase in the amount of information that is processed in these contexts, fueled by advances in computational methods and capacities. The rise of Numerical Taxonomy in the 1960s–1970s (Sokal and Sneath 1963) is a case in point (but see Vernon 1988), and in contemporary Phylogenetic Systematics using advanced computational methods to create sets of phylogenetic trees from large data matrices has become standard (e.g., Felsenstein 2004). These practices of data use, however, give rise to questions regarding, among other things, the criteria by which organismal data can be generated and selected for further use, how to translate the available data into units of the phylogenetic tree (i.e., taxa), and

how to select the correct (or better, preferred) phylogenetic tree(s) on the basis of a particular data set that represents the traits of the organisms under consideration.

In their investigative practices, systematists deal with these problems by invoking a number of assumptions and methodological decisions. A first set of decisions involves the preparation of the data that enter into phylogenetic analyses (see also Scotland et al. 2003: 540–542; Velasco 2013: 990–991). These involve, among other things, the following matters:

- *Character individuation*: Gould and Lewontin, in their famous "Spandrels" paper, criticized the adaptationist program for its failure to recognize that organisms are integrated entities, instead "atomizing" the organism into distinct traits and devising adaptationist explanations for each trait separately (Gould and Lewontin 1979: 585). Something similar happens in phylogenetic analysis: organisms and taxa are represented by sets of discrete (molecular, morphological, physiological, or behavioral) characters that each can assume several character states. But here the question arises how a given organism is best broken down into discrete characters, as organisms aren't simply collections of distinct, predetermined traits (for discussion, see Richards 2003). Examples of two organismal characters used in a recent phylogenetic analysis of bird phylogeny (Godefroit et al. 2013) are "Dentary, dorsal surface, shape in lateral/medial view" and "Mt IV, distal end, lateral surface, accessory crest". The traits are morphological traits (nr. 1328 and 1331 as listed in the online supplementary information of Godefroit et al. 2013) of fossil dinosaur species—the shape of the teeth-bearing lower jaw bone, and the shape of a part of the fourth foot bone, respectively. These have been individuated in a particular way, presumably as this seemed to make the most sense to the researchers involved, but it is clear that these traits could have been individuated differently by focusing on the shapes of different bone parts as seen from different perspectives.
- *Character selection*: Once characters have been individuated (but in practice often already in the individuation process), choices have to be made with respect to which characters yield good phylogenetic signals and thus should enter into the data matrix on which the phylogenetic analysis is built. While some characters are highly informative regarding the phylogeny of the taxa under study, other characters are not.[7] Distinguishing between the two groups involves well-informed decisions on the part of biologists who are highly familiar with "their" groups, including decisions on which similarities probably are homologies (due to common ancestry) and which probably are homoplasies (due to convergent or parallel evolution), and which characters are independent from others (as characters must be independent to yield good phylogenetic signals). In addition, it involves the choice of an outgroup or multiple outgroups that are used as the basis for comparison and to "root" the tree.

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[7] Common characters, for instance, are worse indicators of relatedness than rare characters (Sober 1988: 213).

- *Character coding*: Here, the question is which character states are to be recognized. The corresponding character states for the two characters mentioned above are "flat to convex (0); anteriorly concave (1); concave for most of its length (2)" for the first trait, and "absent (0); present (1)" for the second trait. Here, too, it is clear that different choices could have been made (such as introducing an intermediate state between "anteriorly concave" and "concave for most of its length"), depending on the fossil material that is available. In addition, choices need to be made regarding the determination of character polarity, i.e., the determination which character state is ancestral and which appeared later in evolutionary history (Sober 1988: 29). There are various ways to code character states for use in phylogenetic analyses and while the choice that is made deeply affects the outcomes that one will obtain, no agreement exists on how characters should be coded (Pleijel 1995).

With respect to these three issues, systematists make informed decisions that, however, never settle an issue once and for all. Different decisions remain possible, such that phylogenetic analyses always involve some degree of convention.

A second set of decisions involves the methodology of phylogenetic analyses themselves. The question how data sets are best transformed into phylogenetic trees and the selection of the preferred tree(s) from the set of trees produced in a phylogenetic analysis are important parts of the problem of phylogenetic inference. The number of possible trees grows super-exponentially with the number of taxa: for n taxa the number of possible, fully resolved, rooted bifurcating trees is $(2n-3)!/2^{n-1}(n-1)!$ (Felsenstein 1978a: 28, 2004: 23), which amounts to 15 possible trees for four taxa, 105 trees for five taxa, 945 trees for six taxa, 10,395 trees for seven taxa, and so on. These large numbers of possible trees need to be reduced to a small number of preferred trees. To determine the tree or trees that best represent the data, researchers strongly rely on methodological assumptions, such as the principles of maximum parsimony, maximum likelihood, neighbor joining (the "distance method"), or total evidence, that underwrite the specific way in which data matrices are built and transformed into sets of phylogenetic trees. To some extent, the choice for a particular method consists in the commitment to a particular paradigm or school of research, where different commitments are always possible and debates are ongoing between competing schools (Haber 2009: 236–238; Velasco 2013: 992–996).[8]

A prominent example pertains to the use of the principle of maximum parsimony, which currently is dominant in phylogenetic analysis (see Sober 1983, 1988, and Haber 2009, for extensive discussions of the principle of parsimony). The editors of one of the main journals in the field, *Cladistics*, have recently imposed parsimony as

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[8] Note that for illustrative purposes I am oversimplifying in my description of methodological principles. While commitment to the principle of parsimony implies commitment to a particular school of thought in phylogenetic systematics (namely, Cladistics), within this commitment there still are multiple methods to choose from, such as Camin-Sokal parsimony or Dollo parsimony. Thus, even within one broad school of thought, there are different approaches that yield different results on the basis of the same data (e.g., Felsenstein 1979, 1988, 2004: 73–86).

the preferred methodology for making phylogenetic inferences. "The epistemological paradigm of this journal is parsimony", they write, and "[p]hylogenetic data sets submitted to this journal should be analysed using parsimony. If alternative methods are also used and there is no difference among the results, the author should defer to the principles of the Society and present the tree obtained by parsimony." (Editors 2016: 1). According to the maximum parsimony principle, the preferred tree is the one with the minimum number of character transformations, as this represents evolutionary history with the minimum number of evolutionary changes. This is legitimized by the consideration that it is unlikely that a particular trait evolved many times in separate events—rather, evolution is a process that produces a trait only once or a few times before it spreads through the tree. Using maximum parsimony, however, often leads to branches with a large number of independently evolved convergent traits ("long branches") to be clustered together lacking a basis for such a clustering. The result is that clades are formed based on convergences (homoplasies) rather than on synapomorphies (homologies), and thus encompass branches that may or may not be closely related—a problem called "long-branch attraction" (Felsenstein 1978b, 2004: 114; Bergsten 2005; Haber 2009: 235). Rather than allowing a zooming in onto the correct tree, adding more data only increases the problem as "long" branches become even longer (the part of tree space where this occurs is called the Felsenstein Zone). Assuming maximum parsimony as the principle that guides phylogenetic analysis thus deeply affects tree topologies—on the basis of the principle one obtains different trees than when working with other principles.

The assumptions and methodological decisions that feature in phylogenetic analyses, both with respect to the preparation of the data that enter into the analysis and the methodology used to transform data into sets of phylogenetic trees, thus confer a certain degree of conventionality upon the products of systematic biology—taxa and trees.[9] The choices that one makes deeply affect the outcomes one obtains, and for each of the issues mentioned above alternative choices always are possible. I want to argue that this negatively affects the suitability as information storages of the taxa that are created in phylogenetic analyses for at least three reasons.

First, the taxa that emerge from phylogenetic analyses (which usually are higher taxa, but also can be at the species level on the assumption that species are monophyletic groups of populations) involve a degree of conventionality with respect to which groups are clustered together. Depending on the assumptions used in the analyses, different taxa emerge. This means that—contrary to what some authors have claimed[10]—there generally is no basis to assume that generalizations are possible

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

[10] E.g.: "The erection of (at least approximately) monophyletic higher taxa does, as cladists insist, make a significant contribution to the accommodation of inferential practices in evolutionary biology to relevant causal structures" (Boyd 1999: 183).

over the taxa that emerge from phylogenetic analyses: inferences can be expected to hold over some but not all of the groups that are clustered in a taxon (probably together with some groups that are not clustered in the taxon), but there is no basis to expect inferences to reach exactly over a taxon. The underlying reason is, second, that phylogenetic analyses rely on trade-offs with respect to which data should be prioritized. When assuming the principle of parsimony, for example, the ideal is to find the tree involving the minimal number of evolutionary character state transitions. Usually, though, a tree that involves a minimum number of steps for some characters does not involve the minimum number of steps for other characters, and most of the time it is not possible to find a tree in which all characters are transformed in the minimum number of steps. The principle of maximum parsimony assumes that the tree with overall the minimum number of steps best represents the data, but it may well be that the actual course of evolution involved a minimum number of steps with respect to one set of characters, a higher-than-minimum number of steps with respect to another set of characters, and overall a higher-than-minimum number of steps. The third reason is that the taxa resulting from phylogenetic analyses can be used as basal groups in further phylogenetic analyses, yielding further higher-level taxa, leading to a further spread of inferential problems to further taxa.

Summarizing, the problem of phylogenetic inference is that the taxa produced by phylogenetic analyses to a considerable extent are conventional clusters of organismal groups, as they rest on methodological choices made by investigators. This further weakens the ability of taxa to serve as the bases of generalizations and as information storage units, because there is no reason to assume that generalizations will extend over precisely the members of conventional groups. There is, however, a still deeper problem, which pertains to the adequacy of the Tree of Life as a representation of evolutionary history. I will briefly address this issue in the next section.

5 The trouble with the Tree of Life

The standard visual depiction of evolutionary history has long been a binarily splitting tree. In the only illustration included in the *Origin of Species*, Darwin famously depicted evolution as a bush of lineages fanning out from one point. On the level below the species level in Darwin's picture, splitting was not bifurcating, as Darwin wanted to depict how numerous slightly different forms ensued from a single ancestral form, and subsequently most of these new forms were selected against and go extinct. But at the species level, Darwin's picture was a bifurcating tree, suggesting the currently still widely accepted view of speciation events as consisting in an ancestral species giving rise to two descendant species (where one descendant species can also be conceived as continuing the ancestral species). Haeckel, the main proponent of Darwinian evolution in the German-speaking world, used realistically drawn trees to depict overall evolutionary history in his *Generelle Morphologie der Organismen* (1866) and the evolutionary history of mankind in his *Anthropogenie* (1874). And contemporary phylogenetic systematic methods, too, are based on the assumption that evolutionary history is a binarily branching pattern (Hennig 1950, 1965, 1966). Accordingly, phylogenetic analyses aim at producing bifurcating trees,

and trees that include non-binary splits (in which for instance three new branches emerge from a node) are thought of as not fully resolved trees, for which more data or a better analysis might eventually result in a fully resolved tree.

Many authors have, however, recently argued that dichotomously branching trees, as they are produced by phylogenetic analyses, are bad representations of evolutionary history. Various issues, in particular incomplete lineage sorting (Degnan and Rosenberg 2006) and the occurrence of lateral gene transfer (especially in prokaryotes) that lead to widely occurring mismatches between gene trees and species trees, have been highlighted as problematizing the idea that the history of life on Earth can be represented by a tree-like structure, and taken as the starting point for an ongoing debate about tree thinking in biology (e.g., Doolittle 1999, 2010; Doolittle and Bapteste 2007; Koonin and Wolf 2009; O'Malley et al. 2010; O'Malley and Koonin 2011). As Doolittle (1999, 2010; Bapteste et al. 2009) repeatedly pointed out, lateral gene transfer is so common among prokaryotes that at least for this part of biodiversity—that is, for by far the largest part of evolutionary history and for current biodiversity!—evolutionary history is not well represented by a bifurcating tree.[11] As he put it:

> For most of Life and most of its history, descent with modification is not the simple branching process he [Darwin] envisioned. And in prokaryotic systematics a bifurcating TOL, even if we could be certain about its structure, will not do the work of predicting or explaining phenotypic similarities and differences we expected [...] Microbial *neoDarwinists*, at least, were *demonstrably* wrong, in their expectations and in the conceptual framework that produced them. (Doolittle 2010: 469; italics in original).

The deeper problem is that for prokaryotes (and sometimes for eukaryotes too) genes often have a different evolutionary history than the organisms in which they occur, such that molecular data do not yield patterns that adequately represent evolutionary history at the organism level.

Accordingly, biologists and philosophers are increasingly thinking about evolutionary history as exhibiting a more complex network structure than can be shown in a representation in terms of dichotomously branching trees (Kunin et al. 2005; Bapteste et al. 2009, 2013; Doolittle and Bapteste 2007). Some authors have argued for alternatives to the Tree of Life and have begun to explore network representations of evolutionary history (e.g., Kunin et al. 2005; Bapteste et al. 2013; Morrison 2014; Suh et al. 2015), or have argued in favor of a pluralistic perspective on the representation of evolutionary history with a "forest" of lower-level trees instead of one organism-level or species-level tree (Koonin and Wolf 2009).

Still others have argued that the Tree of Life should be seen as an investigative tool rather than an adequate representation of evolutionary history as it actually occurred, with some authors holding that the tool was useful in past research but is no longer required, and others still seeing uses for it. Doolittle and Bapteste,

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[11] For eukaryotes, however, bifurcating trees often are adequate (Bapteste et al. 2009).

for example, have suggested that the Tree of Life has done its job and can now be discarded:

> Darwin's TOL hypothesis, like most biological theories, is a claim about the process that underlies a pattern. It is important for modern phylogeneticists to remember that reconstructing the TOL was not the goal of Darwin's theory, but rather it was an integral element of his developing model of the evolutionary process. Importantly, this simile prompted generations of scientists to take Darwin's claim that evolution had occurred seriously, for all his lack of a coherent theory of inheritance. The TOL was thus the ladder that helped the community to climb the wall of acceptance and understanding of evolutionary process. But now that we have climbed it, we do not need this ladder anymore. In 2006, our understanding of evolution […] is rich and pluralistic in character and does not require (or justify) a monistic view of the phylogenetic pattern. Holding onto this ladder of pattern is an unnecessary hindrance in the understanding of process (Doolittle and Bapteste 2007: 2048).

On these authors' view, the Tree of Life served two purposes in the early days of evolutionary theory. First, it served as a model for the evolutionary process, depicting (in Darwin's picture in the *Origin of Species*) the process in a simplified way as consisting of a fanning out of a diversity of forms from a single form followed by a culling of many forms, leaving a few in existence to reach species status after a large number of È. Second, it helped the community of biologists in Darwin's time and after to accept Darwin's account of how evolution occurred. Important as these roles were earlier on in the development of evolutionary theory, though, Doolittle and Bapteste hold that the current, much more detailed knowledge of the evolutionary process often is at odds with Darwin's oversimplified picture, such that the picture today is a hindrance to evolutionary research rather than a useful tool.

O'Malley and Koonin, in contrast, have suggested an instrumental view of the Tree of Life and hold that the Tree of Life can still perform important functions as a tool in evolutionary science. As they write:

> From a practical point of view, the TOL [Tree of Life] provides a framework in which to order biological knowledge for both scientific and broader social purposes. It is a tool with which to explore a range of phenomena, some of which it identifies and the rest of which it may indicate cannot be captured by that particular approach. More specifically, the TOL, all its limitations notwithstanding, is necessary as a scaffold for reconstructing scenarios about the evolution of features of organisms (O'Malley and Koonin 2011: 8).

As a framework or scaffold, however, the Tree of Life should not be taken as accurately representing the evolutionary history of life on Earth. Rather, the

tree-like representation of evolution should be seen as a scientific instrument that helps to organize research, provide a background structure for investigative projects, etc. O'Malley and Koonin suggest two ways in which trees can perform this role. First, the Tree of Life and parts of the Tree can be interpreted as evolutionary hypotheses about how organisms, morphological and behavioral traits, genetic sequences, and so on are related to each other. Such hypotheses can be tested and their refutation could give rise to new such hypotheses, new insights into evolutionary processes and new lines of investigation. Second, the Tree could be thought of as a heuristic device (for a similar view, see Mindell 2013). Referring to Whewell's views of heuristics, O'Malley and Koonin suggest that the Tree of Life can have a unifying role by relating phenomena studied in different areas of biology to each other and highlight "the power of the TOL to probe copious data, suggest high-level explanations, and make general sense of the information produced by an explosion of tools, analyses and models in evolutionary biology. Heuristics need not explain or capture everything: their epistemic importance lies in their ability to open up valuable lines of inquiry." (O'Malley and Koonin 2011: 9). The basic idea is that knowledge generated about different areas of biodiversity and using different methods can be connected by mapping it onto a common framework.

The two pairs of authors do not elaborate a detailed account of the tool-function of the Tree of Life in Darwin's times or in contemporary biology (but I will say more on how this tool-function can be realized in the next section). Their main point of agreement (and the point that is relevant in this section) is the observation that the fruitful use of the Tree of Life in biological research does not imply that the Tree of Life correctly depicts evolutionary history (i.e., that it is a real historical entity). This discussion shows, I suggest, that in addition to the problems highlighted in the preceding sections, the basic structure within which taxa are thought to serve as information storage units is problematic too. The taxa that appear in phylogenetic trees quite possibly are building blocks of a profoundly inadequate representation of actual evolutionary history and as such are themselves problematic as representations of any natural order in the living world.

The current debate on the Tree of Life shows a move away from thinking about the Tree (and the taxa that occur in it) as a storage system of information about organisms, in which taxa support inferences about the traits of their member organisms, toward thinking of the Tree and its taxa as performing other epistemic roles. To be sure, the debate is still open and in particular it still is controversial exactly how much lateral gene transfer occurs in eukaryotes and to what extent this affects the adequacy of representations of eukaryote evolutionary history with bifurcating trees (Keeling and Palmer 2008; Danchin 2016; Sieber et al. 2017; Dunning Hotopp 2018). In any case, if lateral gene transfer is indeed widespread not only in prokaryotes but also in eukaryotes, it will add considerably to the problem set of phylogenetic inference, discussed in the preceding section, and thus will make it even more difficult to think of taxa as information storage units.

6 How taxa support inferences

The view of taxa as information storage units that I have examined in this paper involved taxa as groups of organisms over which inferences regarding these organisms' traits were supported. If a taxon holds information about its member organisms, the thought is, this information can be expressed in the form of inferences from species membership to organismal traits. If I know that a particular organism is an *Ornithorhynchus anatinus*, I know *by virtue of the information stored in the species* (i.e., the information that the species name represents) that it its natural habitat consists of rivers, streams and lagoons in eastern Australia and Tasmania, that it eats mainly aquatic invertebrates and small fish, and so on. I have argued that taxa are poor holders of information about organisms in this sense. If this is right, though, it does not necessarily mean that taxa do not play *any* role in information storage and retrieval, or in inferential practices in biological science. I want to conclude with a—very tentative—suggestion as to what the role of taxa in this respect could be.

First, let me step back and briefly address the question what kind of inferences taxa are supposed to support. In Sect. 2, I have pointed out that generalizations over taxa seemed to be stable and reliable because they were causally supported. In this respect, taxa seemed to support generalizations in a similar way as natural kinds are usually thought to do. However, even though some authors continue to think of species and higher taxa as natural kinds (most prominently, Boyd 1999), work in the philosophy of biology has cast severe doubt on this understanding of taxa. Moreover, in Sects. 3–5 I have tried to show that the causal basis of taxa is not of the sort that would support generalizations that reach over taxa. On a view of biological generalizations as causally supported universal statements of the sort "All members of kind *K* exhibit property *p*"—that is, as generalizations of the sort that hold over unproblematic natural kinds—this implies that taxa do not support biological generalizations.

Waters (1998), however, pointed out that many biological generalizations are of a different sort. Many generalizations in biology, Waters argued, are "historically-based contingencies which represent current or former distributions of biological entities of various kinds" (Waters 1998: 6). Waters called such generalizations 'distributions', distinguishing them from causal regularities. Distributions are statements that tell us how traits, organs, structures, behaviors, and so on are distributed through the living world—i.e., in which regions of the Tree of Life (or other representation of natural history) such items are likely to be found. Examples that Waters mentioned include "the prevalence of particular kinds of circulatory systems across taxa", the prevalence of different tissue types in different types of blood vessels (Waters 1998: 6),

> [t]he four year cycle in the number of organisms in Canadian populations of small herbivores, the preponderance of arrowleaf plants with structurally rigid leaves (rather than flaccid leaves) on land and the converse of arrowleaf plants in water, the prevalence of organisms with Mendelian segregation systems among diploid taxa, and the abundance of introns in vertebrate genomes and their absence in genomes of prokaryotes (Waters 1998: 13).

Waters pointed out that distributions are contingent generalizations, not lawlike ones, and that the domains over which they reach vary considerably: distributions can reach over geographical regions, habitats, cell lineages, spatial regions within individual organisms, taxa, and so on (Waters 1998: 13).

I want to suggest that the inferences about the traits of organisms that were mentioned above are best seen as distributions reaching over taxa, and as not causal regularities, and connect this to the function of the Tree of Life as a tool that was discussed in the preceding section. Distributions are statements about how tokens of biological kinds (such as traits, genes, organs, behaviors, etc.) are distributed throughout the biological world. They are "properly explained in terms of evolutionary history" (Waters 1998: 33), as they represent historical contingencies. They represent historical events located at particular points in evolutionary history (i.e., the rise and fixation of a new trait in some part of the Tree at some point in time) and their long-term traces in natural history (i.e., the persistent presence of the trait in some, parts of the Tree for some time after it arose and became fixated). For the reasons specified in Sects. 3–5, the temporal extension of these latter traces (i.e., the parts of the Tree in which traits a conserved) will not generally be coextensive to the temporal extension of taxa. A distribution simply is a generalization that reaches over a part of the Tree of Life from the point at which a trait arises and becomes fixated to the point at which it becomes lost again—points in the Tree that will not generally correspond to the beginning and end points of recognized taxa (Reydon 2006).

Still, I want to suggest, taxa perform a role in this context as what can be called "location markers" in the Tree of Life (or other, less tree-like representations of evolutionary history). Knowledge of an organism's location in the Tree allows us to infer many of its properties if we have sufficient knowledge about the properties of other organisms located nearby in the Tree as well as the level of entrenchment of these properties. In such inferences, however, taxa do not function as kinds (in the way that, for example, the chemical elements function as kinds) over which inferences of the sort "All (or most) members of kind K exhibit property p; organism O is a member of kind K; therefore, organism O will probably exhibit property p." can be made. Rather, the inference is of the following form: "Property p is a locally conserved trait of the organisms in area A of the phylogenetic tree; organism O is located in area A; therefore, organism O will probably exhibit property p." This latter inference is a distribution.[12] Taxa do not occur there as the basis of the inference—in fact, they do not occur in the inferential statement at all. Rather, they feature indirectly as a specification of the area A that is being referred to. The difference between the two inferences mentioned above is that in the latter inference an organism's evolutionary proximity to other organisms features as the basis for inferential statements, whereas in the former inference its membership of a particular kind performs that role.

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[12] Note that it is a particular kind of distribution. On Waters' account, distributions come in various forms, and the distributions that I am considering here are just one such form.

Both kinds of generalizations are important, but they do different kinds of epistemic work and complement each other in this respect. As Waters argued:

> Causal generalizations concern the behavior of theoretical kinds; distributions concern the prevalence of tokens. Causal generalizations are about the causal behavior of actual and possible tokens under actual and possible conditions; they support counterfactual conditionals, contribute explanatory force, and are themselves explained in terms of the causal interaction of components and external elements. Historically based distributions are about the way actual tokens are, and have been, distributed in the world; they are contingent on the course of evolution, provide fruitful information that leads to important advances in biological knowledge, and are explained by historical/evolutionary considerations. Practicing biology involves identifying and explaining both kinds of generalizations. (Waters 1998: 33).

On such a view, which I endorse, it is possible to accept the negative claim I argued for in the preceding sections and that is reflected in the title of the present paper—that it is mistaken to think that taxon membership tells us much about the properties of a taxon's their member organisms—while still seeing taxa as epistemically important. Taxa, on the view I propose here, hold *relational* information about organisms (information about where we find an organism in the genealogical nexus in relation to other organisms), but not *intrinsic* information (information about the morphological, genetic, and behavioral properties of organisms as members of a particular kind). The relational information contained in an organism's taxon membership can be used to infer information of the latter sort.

The role of taxa in inferences is thus best understood as providing supportive knowledge for inferences about the traits of organisms: taxa are not kinds that hold information about their members per se, but location markers that hold information that helps us make inferences from the traits of some organisms to other organisms located nearby in the tree. An important aspect of this view is that taxa retain this location information between different phylogenetic trees and under taxonomic revisions, as the information is relational.[13] This means that it is not a taxon in isolation that plays the role of location marker, but always the taxon in the wider context of a genealogy. It is in this sense that one can think of a tree as a tool for biological science: the tree serves as the map against the background of which taxa can function as location markers. For a tree to be able to perform this role, it does not need to be a realistic or detailed representation of evolutionary history. All it needs to do is to constitute a stable background for statements of the sort, "Organism X is in an area of the genealogical nexus where traits p_1, p_2, p_3, etc. tend to be conserved." Note that this is not a role that is likely to be performed by a single Tree of Life—rather than one tree, we should think of a manifold of phylogenetic trees that trace the distributions of different (genetic, morphological and behavioral) traits through the

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[13] While the content of the location information changes in taxonomic revisions, taxa retain location information as such. When groups are moved in taxonomic revisions, old location information is replaced by new location information.

genealogical nexus and in this way represent different aspects of evolutionary history. This can be taken as a heuristic role in the sense discussed in the preceding section, as it involves the tracing of characters that researchers have chosen to individuate and code in certain ways while other options were available.

7 Concluding remarks

The account presented in the preceding section has several advantages. For one, it provides a way to avoid or at least mitigate the three problems highlighted in the Sects. 3–5. The three problems, I argued, constitute a cumulative challenge to the view that taxa store information about the traits of their member organisms and therefore can serve as the basis of generalizations of the sort that are thought to hold over natural kinds—i.e., generalizations of the sort "Because X is a member of taxon T, it is likely to exhibit properties p_1, p_2, p_3, etc.". The problem of generalization over taxa is tied to taxa performing the role of basis for generalizations. I have argued that reference to taxa in biological generalizations does not play such a role, such that this problem is avoided. The other two problems, the problem of phylogenetic inference and the problem regarding the Tree of Life as a representation of evolutionary history, are tied to the extent to which one thinks that phylogenetic trees should represent actual evolutionary history. On interpretations that view phylogenetic trees as tools to trace trait distributions rather than representations of evolutionary history, the problem of phylogenetic inference becomes less impactful. One still is faced with questions of character individuation, selection and coding, but the consequences of the choices that are made are less severe. Once one accepts that phylogenetic analyses necessarily involve decisions regarding how to individuate traits, regarding what counts as the same trait and what not (e.g., how much toward orange can a bird's feathers be an still count as instantiating the trait "red feathers"?), regarding the selection of traits to take into account, and so on, one can allow for a manifold of trees that represents the distribution of traits that were individuated and selected in different ways. The conventionality of trees and taxa, discussed in Sect. 4, is embraced as a normal feature of scientific tools rather than seen as a problem for achieving the one correct representation of evolutionary history.

The account suggested here also avoids the ongoing debate on the metaphysics of species and other taxa as natural kinds, individuals, or something else. On the view proposed here, taxa simply are parts of phylogenetic trees that are delimited in part by convention—they are analogous to geographical areas on a partial map of a region and perform similar epistemic roles. It also allows for a unified view of species and other taxa. While higher taxa are often not thought of as real units in nature, but merely instrumental units that are useful for imposing order onto biological diversity, species are often considered real entities. The account proposed here treats species and higher taxa equally: all taxa—species as well as higher taxa—are to be treated instrumentally as location markers, i.e., waymarks in evolutionary history that allow us to locate organisms in the vicinity of other organisms in evolutionary history, which in turn allows us to infer knowledge about organisms on the basis of knowledge about their neighbors.

The view presented in Sect. 6 fits well with Hennig's (1950, 1965, 1966) work that defined contemporary phylogenetic systematics. On Hennig's approach, higher taxa are individuated on the basis of unique traits (synapomorphies) that are shared by an ancestral species and its descendant species, such that higher taxa (monophyletic groups) trace trait distributions to some extent. Hennig thought of species as groups of organisms held together by reproduction and gene flow, delimited through time as branches of the genealogical nexus between two splits:

> The limits of the species in the longitudinal section through time would […] be determined by two processes of speciation: the one through which it arose as an independent reproductive community, and the other through which the descendants of this initial population ceased to exist as a homogeneous reproductive community (Hennig 1966: 58).

Although traits are not mentioned here, both for Hennig and in later formulations of the Phylogenetic Species Concept traits play a role in the delimitation of species too. For one, only splits in the genealogical nexus that are accompanied by the origin and fixation of a new trait can be reconstructed by phylogenetic methods. Moreover, Hennig assumed that splits in fact always are accompanied by novel traits:

> If a species […] is split into two mutually isolated communities of reproduction, there is always a change (transformation) of at least one character of the ancestral species in at least one of the two daughter species (Hennig 1966: 88).

Taxa are thus individuated on the basis of unique traits in combination with splits in the genealogical nexus (Reydon and Kunz 2019: 630–631). The organism functions in this context as the bearer of traits that are characteristic of its species. Because they are defined on the basis of unique traits, species and higher taxa will generally trace trait distributions.

Note that the view proposed here has some consequences for the ongoing debate on the role of morphological characters in phylogeny reconstruction (see, e.g., Scotland et al. 2003; Jenner 2004; Wiens 2004; Lee and Palci 2015). The rise of molecular phylogenetics has led researchers to question the usefulness of morphological data for phylogeny reconstruction, leading to views of morphological data as either not important at all or as useful in a supporting role with respect to molecular data. While the view proposed here does not entail a resolution of this debate, it does entail a different perspective on the issue. The debate is taking place against the background of the that phylogenetics' main aims are the reconstruction of evolutionary history and the placing of taxa in a classificatory system—the Tree of Life—that best represents evolutionary history. The debate then revolves around the question how well suited morphological characters are to achieve these aims, given that they are much less ambiguous than molecular traits. If the aim of phylogenetics is taken to be the tracing of trait distributions rather than the representation of evolutionary history, however, this

entails a more prominent role for all traits, morphological and behavioral as well as molecular. This view shifts the focus of phylogenetics to be *about* traits: trees are supposed to inform us about the distributions of genetic, morphological and behavioral traits through parts of evolutionary history, such that traits come to stand at the focus of phylogenetic analyses rather than be seen as merely the basis for tree construction. From such a perspective, morphological traits are on a par with molecular traits.

Species and higher taxa thus do not store information about organisms in the way kinds in the sciences are usually thought to do. But from the considerations presented in this paper it should be clear that this does not mean that taxa do not store information at all. What it means is that their epistemic role in biological science—and in its wake their metaphysical status—should be understood differently from that of kinds of organisms.

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