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Monophyly, paraphyly, and natural kinds

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Abstract. A long-standing debate has dominated systematic biology and the ontological commitments made by its theories. The debate has contrasted individuals and the part – whole relationship with classes and the membership relation. This essay proposes to conceptualize the hierarchy of higher taxa is terms of a hierarchy of homeostatic property cluster natural kinds (biological species remain largely excluded from the present discussion). The reference of natural kind terms that apply to supraspecific taxa is initially fixed descriptively; the extension of those natural kind terms is subsequently established by empirical investigation. In that sense, classification precedes generalization, and description provides guidance to empirical investigation. The reconstruction of a hierarchy of (homeostatic property cluster) natural kinds is discussed in the light of cladistic methods of phylogeny reconstruction.

Introduction

Quine (1994, 42) observed that 'things are similar when they are two of a kind.' Recognition, categorization, and conceptualization of the world take place by sorting similar things into kinds: 'We cannot easily imagine a more familiar or fundamental notion than this, or a notion more ubiquitous in its application' (Quine 1994, 42). There are all kinds of stuff and things in nature: gold, emeralds, and water, tigers, elm trees, and beeches. But how far, exactly, does this similarity relation reach out towards the causal structure of the world, for to be significant, similarity needs to be causally grounded (Shoemaker 2003a)? Quine (1994, 49) cautioned: 'By primitive standards the marsupial mouse is more similar to the ordinary mouse than to the kangaroo; by theoretical standards the reverse is true.' This distinction can be rendered as one rooted in a difference of competence in the use of language: everyday language may use the term 'mouse' to refer to the marsupial mouse also, whereas the technical language of biology allows the term 'mouse' to refer to the ordinary mouse only (Putnam 1996).

Indeed, biology has an elaborate vocabulary to describe and analyze the mistake that occurs if the ordinary term 'mouse' is used to refer to the marsupial mouse also. Putting just the marsupial mouse and the ordinary mouse into a group results in a paraphyletic (or simply non-monophyletic) grouping.

Such a group is said to be unnatural, because it includes some (the ordinary mouse and the marsupial mouse) but not all of the descendants of its most recent common ancestor. The most recent common ancestor of a group that includes the marsupial mouse and the ordinary mouse is the one from which all marsupial and placental mammals originated. Including all marsupial and placental mammals in the group that also contains the marsupial mouse and the ordinary mouse results in a monophyletic, or natural group, for it now comprises the common ancestor and all of its descendants. Putting the marsupial mouse together with the kangaroo instead of with the ordinary mouse also generates a natural, monophyletic grouping, for the marsupial mouse and the kangaroo share a common ancestor that is not also the ancestor of the ordinary mouse.

For Quine (1994), a special branch of science matures if the 'primitive' (unanalyzed, perhaps unanalyzable: Hull 1999) relation of similarity is replaced by a more sophisticated, theoretical concept of sameness. The special branch of biological sciences called systematics is said to mature if non-monophyletic groups are replaced by monophyletic groups (Hennig 1966). I propose to analyze the growth of systematic knowledge (understood, in the present context, as the replacement of non-monophyletic by monophyletic groups) in terms of the deployment of natural kind terms. At the same time, it must be remembered that this present analysis focuses on supraspecific taxa. It does share the enthusiasm (Boyd 1991) for natural kinds, but at this time and in the present context only some aspects of the much more complex issue of the application of natural kind terms to biological species (Boyd 1999) will be discussed. It has been argued that at least in the case of sexually reproducing organisms, the relations amongst individual organisms within a biological species are tokogenetic rather than hierarchical (Hennig 1966), such that the notion of monophyly (and consequently the notion of non-monophyly) does not apply to the species category. How this and other issues bear on the deployment of natural kind terms for biological species will be the subject of a later, more complete analysis.

A biological example

To talk about the world is to cognize and conceptualize the world, to carve it up into different kinds of things or kinds of stuff in the hope that such natural kinds will serve the purpose of causal explanation (Platts 1997). For as was noted by Haack (2000, 231), causal explanation requires a vocabulary 'which classifies things into real kinds,' while Kitcher (1993, 80) emphasized that natural kind terms are 'predicates [that] are associated with properties for use in explanations and in inductive generalizations.' The only problem here is a natural vagueness (de Sousa 1984) of natural kind terms (as becomes apparent if everyday language is compared to the special language of some branch of science), and the observation that any object may be a token of several kinds

(Dupré 1981 1993). As noted by Dupré (1981), biology is a good place to look for examples.

Everyday language will put turtles and crocodiles, lizards and snakes, into a group named 'reptiles,' whereas 'birds' are a group of their own. In the language of biology, this would mean that if turtles and crocodiles, lizards and snakes, are to form a natural group that excludes birds, they must share a common ancestor that is not also the ancestor of birds. But in the 19th century already, Thomas H. Huxley, the most outspoken of Darwin's supporters, voiced the idea that birds might be descended from dinosaurs (Dingus and Rowe 1998). If that is true, then 'reptiles' are non-monophyletic (paraphyletic) without including the birds ('reptiles' would include some, but not all, descendants of the most recent common ancestor of turtles, crocodiles, lizards and snakes). Indeed, the idea that birds are descended from theropod dinosaurs is today (almost) generally accepted (Brochu 2001), such that birds are now being looked at as 'surviving dinosaurs.'

Something had therefore to be done about the term 'Reptilia.' It could no longer be considered to designate a natural (monophyletic) group without including birds, but only to designate an artificial (non-monophyletic) group. Accordingly, some zoologists (e.g. Ax 1984) suggested to drop the name 'Reptilia' from the vocabulary of biology, and to replace it instead with Goodrich's (1916) name 'Sauropsida.' The 'Sauropsida' would be one of two amniote lineages including what was commonly referred to as 'reptiles' plus birds. The other amniote lineage was the Theropsida that included the mammals. This works well for zoologists, because they apply 'Sauropsida' to extant organisms only, using the structure of the heart and aortic arches to distinguish them from Theropsida. 'Sauropsida' thus became the name of a natural (monophyletic) assemblage, whereas 'Reptilia' was recognized as the name of an artificial (non-monophyletic) assemblage. However, in his classification of reptiles, Goodrich (1916) had used in addition to soft anatomy some skeletal features to distinguish sauropsids from theropsids, recognizing that these two separate amniote lineages originated from a 'protosaurian' branch. Part of Goodrich's (1916) 'protosaurian branch' is recognized as amniotes today, rendering the original conception of 'Sauropsida' non-monophyletic from a paleontological point of view. The solution, accepted by paleontologists, is to consider 'Reptilia' the name applicable to a group that includes all reptiles, living and fossil, and birds (the name 'Synapsida' is applied to a group that includes all mammals and their fossil relatives).

What this example illustrates is the 'natural shiftiness of natural kind' terms (de Sousa 1984) relative to different domains of interest. A visitor to the zoo will expect to see snakes and crocodiles in the reptile-house, not in the bird-house. The zoologists who want unambiguity of terms reject 'Reptilia' because of connotations this name had in the past, and replace it with 'Sauropsida.' Paleontologists recognize 'Reptilia' as a 'more familiar' name and therefore want to retain it even if its 'meaning has changed more than any other' in vertebrate taxonomy (Gauthier et al. 1988, 182). But in order to designate a natural (monophyletic) group, the name 'Reptilia' has to be used in a way different from its past use.

Fixing the reference

Putnam (1996; see also Putnam 1992, 2001) devised a theory of direct reference and rigid designation for natural kind terms (hereafter NKTs), according to which NKTs are indexical, i.e., acquire their content from the immediate context of their deployment. Such indexicality has also been called 'ostensive indication,' where reference is fixed through ostension. Ostension establishes direct reference for a (non-empty) proper name, but it can also pick out paradigmatic ('standard': Körner 1970; Kripke 2002) members of a natural kind. Following up on such ostension will initially only establish what Putnam (1996) called the 'stereotype' of a natural kind, where the stereotype corresponds to a description (descriptive properties of the kind). To establish the extension of a NKT requires establishing a 'sameness' relation between putative members of a natural kind as provisionally (defeasibly) indicated by the stereotype. This 'sameness' relation is a theoretical relation as it is part of scientific theory construction, and its establishment may require 'an indeterminate amount of research' (Putnam 1996, 11). Establishment of the 'sameness relation' will offer insights into the causal propensities shared by the members of a natural kind, therewith providing an explanation of the 'nature' of the kind. Causal grounding of a NKT will require ostensive (perceptional) contact, linguistic contact, and the assignment of causal powers to the kind (Sterelny 1996, 104). In summary, 'an object will function as a kind, relative to some theory, only if it gives rise to generalizations that collect together the members of its actual extension. Its so functioning means that these members behave in accordance with properties that may be said to define the kind' (Splitter 1988, 326).

Putnam (1996) acknowledged Kripke's (2002) influence on his views of natural kind term semantics, and as Putnam (1996) did with his concept of stereotype, Kripke (2002, 137) allowed that the properties initially believed to mark out a natural kind 'need not hold *a priori* of the kind; later empirical investigation may establish that some of the properties did not belong to the original sample, or that they were peculiarities of the original sample, not to be generalized as a whole.' Putnam's (1996) analysis of natural kind term semantics moves from a descriptive basis of reference (the stereotype of the natural kind) to a causal grounding of reference (yielding the extension of the NKT). The causal grounding of a name of a species or of a higher monophyletic taxon may require an indeterminate amount of research (Putnam 1996), but the goal would be that 'in order to grasp the sense ['meaning'] of a name of a species [or of a monophyletic taxon] … we have to know the criterion of identity for a species [or monophyletic taxon], namely common descent' (Dummett 1981, 145).

The initial approach to subdividing the world (or cognizing the subdivided world) in terms of species and supraspecific taxa is a classificatory act that is based on description (Devitt and Sterelny 1999); that classificatory act establishes the linguistic use of a natural kind term, where the corresponding natural kind can subsequently become the subject of empirical investigation (Zemnach 1996, 62). According to Kitcher (1993, 95), 'our language develops so that we are able to refer to natural kinds and to specify our references descriptively. In addition, we are able to construct a hierarchy of nature, a picture of what depends on what. Against the background of our categories and hierarchy, we are able to ask significant questions.' It seems possible to interpret Putnam's (1996) analysis such that the initial grouping or classification of things into different kinds is captured by the defeasible 'stereotype,' while subsequent scientific investigation establishes the 'extension' of the natural kind term. The initial grounding of the NKT 'swan' by Linnaeus in 1758 resulted in a stereotype that specified waterfowl of white color; subsequent research by Latham in 1790 led to the recognition that the extension of the NKT 'swan' has to accommodate birds of black color as well. Our view of the reference of the NKT 'swan' did not remain fixed, i.e., restricted to birds of white color [Devitt and Sterelny 1999, 92; which is true if 'swan' is used as a genus name. For once again the 'division of linguistic labor' that was invoked by Putnam (1996, 13) needs to be observed: what the layperson refers to as 'black swan' is for the trained biologist a separate species].

What such natural shiftiness of natural kind terms (de Sousa 1984) indicates is that at least in biology, the initial grouping of things into kinds (natural kinds for monophyletic groups; nominal kinds for paraphyletic groups) is a classificatory act based on descriptive reference that precedes generalization based on causal relations. The natural kind term 'reptiles' was used initially to designate 'cold-blooded' (poikilotherm) animals with a scaly skin etc.; subsequent scientific investigation established the extension of 'reptiles' as a group of organisms with a common evolutionary origin, which includes not only 'cold-blooded' animals with a scaly skin, but also warm-blooded animals with feathers. According to the criterion of monophyly introduced by Hennig (1950, 1966), the reference of the term 'reptiles' was initially fixed on a paraphyletic group. Following the 'cladistic revolution in systematics' (Hull 1988) and subsequent research, the extension of the term 'Reptilia' changed *a posteriori* (Boyd 1991, 1999) to include birds.

This is a change of meaning, which is far more radical than the de-whaling of fish. The latter is said not to have changed the meaning of 'fish' (Mellor 1996, 70; 'fish' is not a natural, rather a nominal kind term in modern biology), because the mistaken multiple grounding of the NKT 'fish' in whales is 'insignificant in number relative to those [groundings] in the original kind' (Devitt and Sterelny 1999, 90). The same is not true for the 'feathering' of reptiles (Padian 1998; Qiang et al. 1998), hence the controversy over the use of 'Sauropsida' instead of 'Reptilia.' Such significant shiftiness of natural kind terms is certainly difficult to assimilate to traditional (conservative) conceptions of natural kinds (e.g., Ruse 1987; Hacking 1991; where natural kinds have essential properties), but it is well worth investigating in the context of contemporary systematics of higher taxa and in relation to the non-traditional property cluster concept of natural kinds (Boyd 1991, 1999). For this concept also accommodates the fact that the juveniles of the (European) white swan are neither white, nor black, but speckled brown.

Beyond rigidity[1]

The biological entities to which NKTs have traditionally been applied are species. Their treatment as natural kinds stands in contrast to their treatment as individuals (Hull 1999, and references therein), a debate which will have to be the subject of a later analysis. Here, the focus will be on the concept of rigid designation that was invoked by Kripke (2002) and Putnam (1996) for NKTs (but see Soames 2002), and how this concept plays out for NKTs that are applied to historical entities such as species, or supraspecific taxa. The species category is more helpful in this context than that of supraspecific taxa, because the introduction of a species name requires the designation of a type specimen. For Kripke (2002) and Putnam (1996), rigid designation results from 'link-to-link reference-preserving chains' of communication (Hull 1988, 497), a scenario that 'should sound suspiciously familiar' to systematists who are familiar with the 'type specimen method' (Hull 1988, 497).

Initially developed for proper names (and under the species *qua* individuals thesis, species names are proper names), Kripke's (2002) argument starts from an act of baptism. This act rigidly ties the proper name to an individual (e.g., the precise egg and sperm from which Aristotle originated: Sober 1980) through a link-to-link reference-preserving chain of subsequent use of that name. With his concept of rigid designation, Kripke (2002) was able to show that (ordinary) proper names behave differently in modal contexts than definite descriptions. By analogy, the naming of a species can be seen as an act of baptism, and through a link-to-link reference-preserving chain of communication, the chosen species name is said to remain rigidly attached to the species of which the designated type specimen is the paradigmatic exemplar. Following Kripke (2002) and Putnam (1996) who both concluded that rigid designation is also characteristic of NKTs, one could argue that species names rigidly designate species.

The theoretical benefit of treating a species name as a rigid designator lies in the fact that the name would rigidly designate the same historical entity, one which is subject to continuous variation and transformation through space and time and which therefore could not equally well be captured by a description, since the latter could capture a space-time-slice only. Hull (1988, 499) draws the

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[1] The title of this section is borrowed from Soames (2002).

distinction between species names as rigidly designating proper names, and species diagnoses as definite descriptions, and finds the two to behave differently in temporal context. However, the naming of a species and designation of a type specimen is not just an act of baptism, nor based on mere ostensive indication, but is a consequence of scientific theory construction (Mellor 1996, 74). The selection of a type specimen does not fix the reference of a species name in the same way in which, according to Putnam (1996), a sample of (local, i.e., this-worldly) water fixes the reference of the term ‘water’ (H_2O rather than ‘XYZ’). Systematists do not pick out some (supposedly) paradigmatic specimen from some natural population by ostensive indication, and attach to it a new species name in an act of baptism. Instead, they name a new species and designate a type specimen for it only after they have reached some degree of understanding as to what the distinctive properties of the new species are.

Systematists acquire good reasons to believe that they are dealing with a new species on the basis of extensive comparisons of their sample of new specimens with samples of what appear to be closely related, previously known (described) species and their type specimens. It is only at that stage of investigation that systematists choose as type specimen the one they believe best exemplifies the characteristics of the new species. In that capacity, the type specimen is a paradigmatic exemplar of the species it represents. The type specimen is exactly what its name says: a token of a type – where the type is a property cluster natural kind that can accommodate the (ontogenetic, individual) variability that is characteristic of biological species.

According to the ‘International Code of Zoological (and Botanical) Nomenclature’ (Blackwelder 1967)[2] a species name *A* and its author remain forever attached either to the type specimen *a* and the sample from which it was chosen, or to the sample which a systematist – following taxonomic revision – believes to be exemplified by the type specimen *a*. A taxonomist’s sample is not a sample in the statistical sense, but often a mixed ‘series’ of specimens taken by different people using different collecting techniques at different times and in different places (Blackwelder 1967, 284). But such a series can also represent a local population sampled at once specific point in time (constituting a type-series that comprises the holotype and paratypes), and in the case of very rare species, the sample that is initially named may contain the type specimen only. Any extension of species names beyond this use is a matter of potentially changing expert opinion, and that opinion may change as a consequence of ongoing research. The reference of species names can change over time, for the ‘semantic value’ (Evans 1982, 8) of a species name is not a type specimen and the sample from which it was chosen, but the species that is believed to be represented by the type specimen and the associated sample (Blackwelder 1967, 229). The original description of a new species may amount to not much more than a stereotype, and Putnam (1996, 11) cautioned that ‘to fill in the stereo-

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[2] The PhyloCode (Cantino and deQueiroz 2003) currently under discussion is designed to replace these rules, but it has not yet dealt with the species problem.

type' of a natural kind term and thus to establish its extension may take an indeterminate amount of research. The extension of a natural kind term is always established *a posteriori* (Boyd 1991, 1999), as a consequence of scientific theory construction, and the same is true of species names. Previously named species may become the object of taxonomic revision, which may reveal that the samples available in natural history museums that were originally believed to represent two, or even more, different species all represent one single species. In such a case, the oldest available species name takes priority, while younger species names are listed as synonyms of the older name. The link-to-link reference-preserving chain still attaches the author and the name she introduced to the type specimen and the sample from which it was chosen, but the synonymized species name does not 'mean' the same thing anymore, because its referent is not identical with the referent of the name that takes priority (synonymy in taxonomy does not imply cognitive identity; for example, two synonymous species names may originally have been introduced to refer to two species with non-overlapping distributions). And surely nothing prevents future taxonomic revision to recognize that the previous lumping of species *A* with species *B* was unjustified, that *A* and *B* do after all represent different species. Systematists have been classified as 'splitters' and 'lumpers' (Simpson 1961, 138). So the possibility arises, and it happens all the time in taxonomic practice, that species name *B*, first synonymized with species name *A*, is later resurrected, and the type specimen of species *B* becomes a paradigmatic exemplar of its kind again.

In conclusion, it is not the type specimen that fixes the reference for species names. Instead, it is the establishment of reference for species names that provides the context for the designation of type specimens. Only if taxonomy were a 'finished' science would it be possible to claim that species names rigidly designate species via the 'type specimen method' (Hull 1988). As long as taxonomists are still engaged in seeking the correct extension for species names, and that may take forever, species names have the potential to designate the entities evolutionary theory refers to as species. But within that reference potential (Kitcher 1993),[3] reference can potentially shift back and forth. The same is true of names for supraspecific taxa: reference of the name 'Reptilia' shifted over time as discussed above.

A hierarchy of natural kinds

Monophyletic groups form a nested hierarchy called the tree of life. If the names of monophyletic groups are related to natural kind terms, natural kinds of that type (monophyletic groups) must likewise form a nested hierarchy. The NKT 'swan' applies to a higher hierarchical level than the species names 'Australian

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[3] Devitt (1997, 166) used the concept of 'partial reference' to deal with the problem of the confused application of species names.

black swan' and 'European white swan'; the NKT 'reptiles' again applies to a higher hierarchical level than the NKT 'birds,' because according to modern standards, birds are a subgroup of reptiles (birds are nested within reptiles). In the context of systematic biology, the shiftiness of NKTs is thus seen to play out relative to a hierarchy of groups within groups, or kinds within kinds.

If the nested hierarchy of monophyletic groups is to be conceived of in terms of natural kinds, then it must be possible to have a nested hierarchy of natural kinds (Dupré 1981, 1993), such as the one sketched by Platts (1997). For Platts (1997), natural kinds are classes of naturally occurring things, such that the properties that mark out such natural kinds require law-based explanations. These properties, subject to lawfulness, are what determine the members of a natural kind via the 'sameness' relation, which Platts takes to be the identity relation. However, the sameness' relation is not a semantic (analytic), but rather an empirical relation (Schwartz 1979), which imparts the appropriate weakness, even defeasibility, on the concepts of lawfulness and identity (see further discussion below). Therefore, natural kind classifications are 'explanatory promissory notes' (Platts 1997, 270) to be met, if at all, by empirical investigation of the natural world.

In a hierarchy of natural kinds, a lemon is not only a member of the natural kind 'fruit,' but also a member of the natural kind 'citrus fruit' (which is but one of several natural kinds that are members of the kind 'fruit'). According to Platts (1997), the point of distinguishing lower level natural kinds (lemon) from higher level natural kinds (citrus fruit, fruit) is readily understood if natural kind classifications are closely connected to causal explanation. Platts (1997, 272) distinguished the explanatory range from the explanatory power, and noted that as one proceeds within an inclusive hierarchy of natural kinds from more inclusive levels (fruit) to less inclusive levels (citrus fruit, lemon), the explanatory range decreases while the explanatory power increases. An inclusive hierarchy of natural kinds requires that all the kinds included have at least some causal property (properties) in common, but the level of inclusiveness at which a natural kind is accommodated in such a family tree of natural kinds still remains a matter of empirical (*a posteriori)* discovery (Platts 1997, 274).

Empirical discovery relates to interest: it is the interest that fixes the 'explanation space' (Platts 1997, 277) of a chemist, or of a biologist. The scientific investigation of the causal properties of natural kinds therefore proceeds relative to a domain of interest for Platts (1997), while for Boyd (1999), research into the causal properties of natural kinds seeks accommodation to a certain disciplinary matrix. Natural kind classifications within science are grounded in the investigation of nature with an eye to providing law-invoking explanations. But if lawfulness must underlie the explanatory role played by NKTs, and if that lawfulness renders NKTs rigid designators (Putnam 1992, 1996, 2001; see also Kripke 2002), then – according to Dupré (1981) – NKTs cannot be deployed in biology in the same way as in physics or chemistry, because 'biological terms are not at the right level of theory' (de Sousa 1984, 573, n. 17; see also Rosenberg 1994). Lawfulness translates into generalizations with conterfactual force, and that comes in degrees for biological NKTs (Griffiths 1999). Consequently, an adequately weak sense of 'natural law' must be invoked for biological purposes (Rosenberg 1994; see also Mahner and Bunge 1997).

Traditionally, natural kind terms are terms that figure in natural laws: a kind is natural as opposed to artificial 'if one or more of the properties that characterize *all* its members figure in a small number of simple general laws' (Rosenberg 1994: 48; emphasis added). This Millean notion of a natural kind is a very strong one as is the notion of lawfulness tied to it, and it conflicts with the currently popular notion that such universal laws of nature do not exist, especially not in biology (Rosenberg 1994). If there was a 'big bang,' if the physical universe is evolving as well, such universal and timeless (e.g., Hull 1988, 78–81) laws that 'cannot mention particular places, times, or things' and that 'are supposed to be true everywhere and always' (Rosenberg 1994, 116) cannot exist even in physics (Mahner and Bunge 1997). By contrast, it has been recognized that 'there are large subfields within biology that appear to lack any distinctive general principles of their own. The generality that they achieve seems to be attained through the repeated use of explanatory patterns' (Kitcher 1993, 81). Evolutionary biology seems to be a prime candidate for such a subfield of biology, but if the 'repeated use of explanatory patterns' is successful in evolutionary biology, it means that this discipline also deals in causal relations, just not in universal ones. Natural kind terms that apply to historical entities such as monophyletic taxa must therefore be tied to a weaker notion of lawfulness. Ultimately, evolutionary biology may deal in what has been called 'singular causal statements' (Shoemaker 2003b, 232) that necessarily refer to specific points in time and space, but nevertheless conform to a 'repeated explanatory pattern.' 'A singular causal statement does not commit one to the claim that the instantiation of the relevant properties in relevant similar circumstances always produces the effect that it did in the case at hand; for the laws governing these properties may be statistical, the powers to which the properties contribute may, accordingly, be statistical tendencies and propensities, and the causation may be non-necessitating' (Shoemeker 2003b, 232). That seems, indeed, the appropriate way to conceptualize the lawfulness invoked in evolutionary biology. In a theatrical gesture (Rudwick 1972), the early 19th century paleontologist and functional anatomist Georges Cuvier prepared what appeared to be the incompletely exposed skeleton of a fossil marsupial in public to demonstrate the counterfactual force inherent in the NKT 'Marsupialia': further excavation of the fossil duly revealed the previously predicted presence of the marsupial bones, which by comparison with living marsupials Cuvier believed to be necessarily correlated with the presence of an abdominal pouch.[4] However, not every marsupial species

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[4] Cuvier presented this test of the predictive power of comparative anatomy in order to demonstrate the – in his view – lawful functional correlation of all parts of an organism, which would render gradual species transformation impossible.

sports an abdominal pouch to carry their young, nor is the presence of marsupial bones in the pelvis restricted to marsupials alone among mammals – and the marsupial bone is reduced in the Tasmanian wolf. The counterfactual force of NKTs deployed in the context of evolutionary theory comes in degrees (Rosenberg 1994; Griffiths 1999).

A hierarchy of natural groups

According to Darwin (1859, 413) 'the grand fact in natural history of the subordination of group under group … is in my judgment fully explained' on the theory of evolution. Darwin's domain of interest relative to which he sought a causal explanation for the natural hierarchy of groups within groups was descent with modification. Arguing from a philosophical, not from a biological, perspective, Dupré (1981, 1993) was less convinced. Exploiting the indeterminacy of biological NKTs relative to various domains of interest such as agriculture, horticulture, gastronomy, zoo management, wildlife management and conservation, etc., Dupré (1981, 1993) found that the same biological entities function satisfactorily as referents for explanatory NKTs in a multitude of different ways and within many different hierarchies. Dupré (1981, 73) calls 'taxonomic realism' the view that holds that there is only 'one unambiguously correct taxonomic theory.' But for him, Darwin's (1859) theory of variation and natural selection dispensed of the prerequisite for such a uniquely and unambiguously correct taxonomic hierarchy, for natural entities such as species, genera, etc., do not share essential properties. From this, Dupré (1981, 88) concluded that 'there are no privileged properties or relations by means of which these [species] can be sorted unambiguously and exhaustively into objectively significant classes.' If none of these relations are privileged, the result will be a promiscuous realism (Dupré 1993) that 'derives from the fact that there are many sameness relations that serve to distinguish classes of organisms in ways that are relevant to various concerns' (Dupré 1981, 82).

To escape from such a promiscuous realism, Wilkerson (1988; see also Wilkerson 1993) referred back to the 'division of linguistic labor' (Putnam 1996), as he invoked the difference between ordinary (everyday) language and technical (scientific) language. Horticulturists, agriculturists, cooks and zookeepers just don't speak the same language as the botanical or zoological expert taxonomist. Dupré (1989, 249) countered that even in cases where there seems to prevail a genuine correlation between ordinary language terms and terms of scientific taxonomy, 'this correlate is generally not a species' but a higher, more inclusive taxon (see the argument about 'swan' as opposed to 'European white swan' and 'Australian black swan' presented above). Even more, he drew attention to the important point that 'since the overwhelming consensus of contemporary biologists is that taxonomy should be grounded in evolutionary relationships rather than structural or morphological facts, *there is no reason to expect that biological kinds can satisfy both these disjuncts*' (Dupré 1989: 249, emphasis added; see the discussion in concluding section).

Hennig (1950, 1966) likewise recognized that in biology, species could be grouped in many different ways. For holometabolous insects, morphology might group larvae with larvae, and imagoes with imagoes, in separate and possibly different hierarchies, just as in molecular systematics, different genes might group the same organisms in separate, and possibly different hierarchies. On morphological grounds again, tetrapods might be grouped into kinds with and without limbs. Biogeographers group species into palearctic and nearctic kinds, marine biologists group species into pelagic and benthic kinds, ecologists group species into carnivorous and herbivorous kinds, etc. But in contrast to Dupré, Hennig (1950, 1966) felt strongly that among all those possible groupings, one had to be privileged, and that is the genealogical hierarchy, for it is the one to which all other groupings ultimately relate to. However, again like Dupré (1981), Hennig (1950) realized that the genealogical system had to be parasitic on some other criteria that would initially provide a sameness relation that groups species hierarchically. From the perspective of his own research program, Hennig (1950, 26) concluded that the genealogical system piggybacks on morphological criteria of similarity (see Rieppel 2003, for further discussion).

In reference to Wilkerson (1988), it could be said that Hennig's (1950, 1966) request was to replace non-monophyletic groups named by ordinary language with monophyletic groups named by the scientific language of systematics. But whereas a monophyletic, or natural, group is defined as one that includes the ancestor and all of its descendants, such a group is at least initially marked out not on the basis of the underlying causal process of descent with modification, but on a descriptive basis that predicates morphological (or molecular) properties of the sample that is interpreted as paradigmatic of a natural kind. These properties require causal grounding.

The reconstruction of phylogeny

Donellan (1983) drew an important distinction with respect to Putnam's(1996) identification of NKTs as indexicals. Ostensive indication can establish direct reference for (non-empty) proper names (whether as rigid designators or otherwise), because 'nothing about "important physical properties" is needed or used in Kripke's arguments about proper names' (Donellan 1983, 96). In contrast, the 'sameness' relation that is required to establish the extension of NKTs is not indexical, but theoretical instead, a matter of scientific investigation and theory construction. So the question then is how systematists establish the 'sameness' relation in their search to replace non-monophyletic with monophyletic groups. Or, in other words: how do they render genealogical relationships 'epistemically accessible' (Sober 1981).

Privileging the genealogical over all other hierarchies for the grouping of species means that the domain of interest of scientific taxonomy is phylogeny. If monophyletic taxa are natural kinds, then the explanatory function of their names is genealogical: the 'shared nature' of a monophyletic group *qua* natural kind is 'a certain evolutionary origin' (Devitt and Sterelny 1999, 88). As argued by Sober (1981), theories of evolutionary transformations generalize over properties, and Sober's (1981) way to render these properties epistemically accessible is by means of his principle of causal efficacy (Sober 1982), i.e., by fitness values and selective values for properties relevant to the theory of natural selection.

But modern systematics does not individuate properties by means of selective values or fitness values. Instead, it is claimed that 'cladistic analysis can proceed from a list of arbitrary measurements by looking for congruence among the evolutionary trees produced by different measurements and thus "bootstrapping" itself into a reliable character set' (Griffiths 1999, 225). Or, as stated by Kluge (2003a, 236; emphasis added; see also Kluge, 2003b): 'It can be *anything* that leads to a testable hypothesis' of a putatively shared property, where the test is primarily that of congruence. The crucial point here is the appeal to a test, and potential refutation, of taxonomic characters marked out by character statements which predicate properties of organisms that serve as 'operational taxonomic units' or as representatives of terminal taxa.

Cladists initially recognized that congruence, the mere coherence of character statements relative to a hierarchy, although a necessary condition for phylogeny reconstruction, is not also a sufficient condition. They therefore searched for repeated patterns amongst different sets of character statements (Rieppel and Grande 1994), following Whewell's maxim cited by Ruse (1988, 54; see also Ruse 1987): 'The Maxim by which all Systems professing to be natural must be tested is this: – that *the arrangement obtained from one set of characters coincides with the arrangement obtained from another set*' (Whewell's italics). This search for repeated patterns has been turned into the 'total evidence approach' (Kluge 1989) that combines all sets of data for simultaneous analysis (Nixon and Carpenter 1996). The practice of simultaneous analysis robs the method of phylogeny reconstruction of its property of reciprocal illumination in the sense of Whewell's maxim, since all that can obtain from such simultaneous analysis are 'centers of congruence' relative to a hierarchy over the totality of character statements available at the time of analysis. These 'centers of congruence of characters' or, more precisely, the 'centers of coherence of character statements' that refer to co-instantiated sets of properties are interpreted by Boyd (1999: 181) as '(representations of) loci of evolutionary stasis,' islands in morphospace so to speak. And as far as morphology is concerned, the theoretical relevance of these centers of congruence lies in theories of evolution, of development, and of inheritance: homeostatic mechanisms that are responsible for the co-instantiation of the properties marked out by the coherent sets and sub-sets of character statements (Boyd 1999; Wilson 1999). Developmental homeostasis (Dobzhansky 1970;

Wicken 1984),[5] developmental constraints (e.g., Alberch 1982), and ontogenetic entrenchment (Wimsatt 1986; cf. 'burden' in Riedel 1977; 'canalization' in Waddington 1957), are the causal mechanisms that are believed to keep these islands afloat yet anchored in morphospace. Causal efficacy in terms of homeostatic mechanisms of inheritance and development is what renders shared properties relevant for phylogeny reconstruction above the species level epistemologically accessible (Sober 1981), and the degree of developmental homeostasis or generative constraint or entrenchment determines the degree of projectibility of the predicates that refer to those properties for as yet unobserved members of the same kind. The degree of projectibility of those predicates thus translates into the degree to which natural kinds support generalizations with counterfactual force (Griffiths 1999). However, the initial subdivision of morphospace into centers of coherence of character statements that refer to 'anything' or 'arbitrary measurements' in a simultaneous analysis corresponds to the classificatory (or descriptive) phase of the project of phylogeny reconstruction only. It yields no more than a stereotypical (sensu Putnam 1996) hierarchy of kinds within kinds. To establish this hierarchy as one of natural kinds requires going beyond the descriptive phase and towards the investigation of the causal mechanisms of inheritance and ontogeny.

Taxonomic characters versus properties

Systematic biology aims at replacing artificial (non-monophyletic) groups by natural (monophyletic) groups. This can be rephrased, in a metalanguage of biology (Ruse 1987, 227; see also Hull 1999, 27, who stated that 'As philosophers we do not *do* science. We comment on it.'), that systematic biology strives to replace artificial (nominal) kind terms with NKTs. If this is true, then supraspecific taxa are not individuals, as is argued to be the case for species (e.g., Hull 1999). If supraspecific taxa are natural kinds, they cannot be anything else but homeostatic property cluster natural kinds (Boyd 1999). In phylogenetic analysis it is preferred that supraspecific taxa share one or several characters (properties) uniquely (i.e., not also shared by other higher taxa), but it is entirely acceptable that a supraspecific taxon shares no character (property) uniquely. There is therefore no requirement for 'necessary and sufficient' properties for a homeostatic property cluster natural kind that is a supraspecific taxon. As such, higher taxa as natural kinds are defined *a posteriori*, and therefore are always subject to potential empirical revision (Boyd 1991, 1999). The only requirement is that the homeostatic property cluster kind be

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[5] On developmental homeostasis, see Dobzhansky (1970, 38; normal development under a range of environmental and genetic disturbances, as contrasted with 'developmental instability': Polak 2003), and Wicken (1984: 106; 'homeostasis is achieved through organizational complexification' – compare this with the internal integration of developmental modules discussed in the text further below).

natural to the degree that 'it is possible to make better than chance predictions about the properties of its instances' (Griffiths 1999, 216), as Cuvier was able to do with respect to the presence of marsupial bones in a partially exposed fossil from the quarries of Montmartre.

However, such radical contingency (Boyd 1991) for a supraspecific taxon that is a homeostatic property cluster natural kind has important consequences. First, if no necessary properties (uniquely shared characters) are required, then there results some indeterminacy about the extension of a homeostatic property cluster natural kind (Boyd 1991). If membership in a natural kind requires the conjunction of certain properties, then all these properties are individually necessary and jointly sufficient to mark out the extension of the corresponding kind term. The radical contingency of homeostatic property cluster natural kinds requires no conjunction of any properties shared by the kind. This consequence is perfectly well accommodated (Boyd 1999) by biological species that evolve in a gradually changing world [if biological species are treated as homeostatic property cluster kinds, instead of as individuals (Boyd 1991, 1999)], but it is not that easily accommodated by the hierarchical structure of higher taxa relationships, for it results in some indeterminacy of the requirement of monophyly (see below for further discussion).

Second, the definition of a NKT is meant to be explanatory (Glock 2000, 111), i.e., to relate 'kindness' to causally rooted properties, which for higher taxa would be captured by the concept of developmental homeostasis, developmental constraints, and/or generative entrenchment. These are causal mechanisms that underlie phylogenetically informative morphological characters. But if in an initial step 'arbitrary measurements' (Griffiths 1999, 225), indeed 'anything' (Kluge 2003a, 236) can be fed into an analysis that searches for centers of character congruence, or centers of coherence of character statements predicating properties of a representational sample of the kind, then the question emerges as to which degree the resulting diagnosis (not an intensional definition, but an extensional list of potentially disjunct characters) of such groupings will be explanatory. This in turn will affect the predictability of diagnostic characters (the projectibility of the corresponding predicates) for as yet unobserved members of a particular higher taxon.

In contemporary systematics, the explanatory power of a hypothesis of relationships is measured in terms of its consistency with the data (i.e., coherence of the character statements relative to a hierarchy): it increases with an increasing number of congruent and a decreasing number of incongruent characters (character statements that are coherent or incoherent relative to a hierarchy). The congruent characters are the ones believed to have been inherited from common ancestry (homologies), the incongruent (homoplastic) characters are believed to have evolved independently from one another, through convergence, reversal, or chance. Explanatory power measured in terms of consistency (congruence, coherence) only is a quantitative relation between sets and subsets of coherent versus incoherent character statements

(Patterson 1982). Many systematists view the phylogenetic hypothesis that is supported by the largest number of congruent characters to also have the largest explanatory power: 'Simultaneous analysis … produces the *best-supported* hypotheses' (Nixon and Carpenter 1996, 237, emphasis added). In contrast, Farris (1983; see also Kluge 2003a) argued that explanatory power does not reside in the more, or less, reliable projectibility of properties that are linked to common ancestry on the basis of causal mechanisms of inheritance. Such an argument would have to rest on the empirical presupposition that the greater the number of character statements that cohere relative to a hierarchy, the greater is the likelihood that the corresponding characters have been inherited from a common ancestor. Instead, explanatory power increases if a phylogenetic hypothesis minimizes assumptions of homoplasy (Farris 1983; see also Kluge 2003a). Farris' (1983) argument recognized that while the coherence of character statements in support of a hypothesis of relationships is a necessary condition for phylogeny reconstruction, it is not also a sufficient one. Although congruent characters may indeed be inherited from common ancestry, they might also have evolved independently from one another through parallelism (Farris 1983). Since the distinction between homology and parallelism cannot empirically be drawn for congruent characters, Farris (1983) concluded that mere coherence of character statements is not sufficient to support a hypothesis of relationships, but that the incoherence of character statements certainly undermines hypotheses of relationships. The argument is not that coherence of character statements relative to a hierarchy lends support to that hierarchy as a natural one; the argument is that incoherence undermines a hierarchy. Farris' (1983) claim is that explanatory power increases if the number of *ad hoc* hypotheses (explanations) of homoplasy (convergence, reversal) is minimized. The argument therefore is not which hierarchy of natural kinds is most closely aligned with the causal structures of the world, but rather which alternative hierarchies of groups within groups are to be rejected on grounds of incongruence. The argument is about homoplasy, not homology (Wiesemüller et al. 2002). This is why 'anything' (Kluge 2003a, 236) seems acceptable as a character in phylogeny reconstruction, for there is no ambition to reconstruct the tree of life in terms of a hierarchy of natural kinds that support generalizations with counterfactual force. The aim is only to find the 'least falsified' (Kluge 2001, 327) hierarchy amongst all those possible for a finite number of terminal taxa.

In contrast, Platts' (1997) analysis of the hierarchy of natural kinds distinguishes explanatory scope from explanatory power while also emphasizing the reliability of the projectibility of properties: the smaller the explanatory scope, the larger the explanatory power. This is because any property that can be projected for an including taxon (natural kind) can also be projected for the included taxon, but not the other way around. The NKT 'lemon' plays an explanatory role not only for the natural kind lemon, but also for the natural kinds citrus fruit, fruit, etc., but not the other way around. Explanatory power as related to a hierarchy of natural kinds is meant to go beyond a mere empirical presupposition of common ancestry based on the number characters and degree of their congruence. It is a 'promissory note' (Platts 1997: 270) to be met by empirical investigation. The radical contingency of homeostatic property cluster natural kinds will never allow for sharp boundaries, it will not allow universal lawfulness of the causal relations in which NKTs are believed to be grounded. But theories of transformation, development, and inheritance, issuing such concepts as 'developmental homeostasis' (Dobzhansky 1970; Wicken 1984), 'developmental constraints (Alberch 1982), 'burden' (Riedel 1977), 'generative entrenchment' (Wimsatt 1986) and 'canalization' (Waddington 1957) predict the boundaries of more inclusive natural kinds to be sharper than those of less inclusive natural kinds. This is based on the idea of von Baerian recapitulation, where characters that mark out kinds of higher taxonomic rank (of greater inclusiveness) appear earlier in development, and that earlier developmental stages carry a heavier 'burden' because later developmental stages depend on them and hence are less subject to evolutionary change. This would mean that projections of the properties that mark out natural kinds of higher taxonomic rank (of greater inclusiveness) are more likely to be met than projections of properties that mark out natural kinds of lower taxonomic rank (of lesser inclusiveness). Although highly intuitive, such is not necessarily the case (Larsson 2000; Raff and Raff 2000). What increases the reliability of projections of properties (what increases the counterfactual force of NKTs) is rather the degree of internal integration of developmental modules of morphology (in the case of morphological characters) largely independent of taxonomic rank (Larsson 1998; Wagner 1989, 2001; Raff and Sly, 2000; Geeta 2003; Klingenberg et al. 2003).

Coherence of character statements relative to a hierarchy, congruence of the corresponding characters is a necessary, but not a sufficient condition of phylogeny reconstruction. The natural kinds that are marked out by coherent sets of character statements need to be causally grounded (Putnam 1996). The investigation of the (degree of) developmental integration of all, or even most, characters used in higher level systematics may be a theoretical desideratum, but is a practical impossibility. However, it is possible to do better in the search for a hierarchy of natural kinds than to start from 'arbitrary measurements' (Griffiths 1999) or simply from 'anything' (Kluge 2003a). If the reference of a NKT is initially fixed in terms of a stereotype based on description (Putnam 1996), then that stereotype will provide guidance to empirical investigation that will determine the extension of the NKT. In morphology, operational criteria of homology such as topology and connectivity have empirically proven to be eminently useful in the reconstruction of the hierarchy of life (Remane 1952; Riedel 1977), because they are (to various degrees and ultimately defeasibly) rooted in ontogeny (Rieppel and Kearney 2002). Development results in pattern formation (the spatial arrangement of differentiated tissues: Gilbert 1988), and comparative morphology analyzes these patterns in terms of topology and connectivity. Raff and Sly (2000, 102) noted of 'developmental modules' that 'they occupy specific physical sites within the embryo' and 'exhibit varying degrees of connectivity to other modules within the embryo.' Just as criteria of homology provide a guide to morphological comparison, so can secondary structure information provide a guide to the alignment of gene sequences (e.g., Kjer 1995; Olson and Yoder 2002).

Stasis, homeostasis, and change

Some systematists argue that homeostatic property cluster kinds (Boyd 1991, 1999) cannot be accommodated by evolutionary theory, that species and supraspecific taxa cannot therefore be such kinds: 'in being homeostatic, such kinds cannot evolve' [Grant and Kluge 2004: 25; see also Kluge (2003a, 234): 'whatever is "homeostatic" cannot, by definition, evolve']. The lexical meaning of 'homeostasis' is the maintenance of a dynamically stable internal environment in an open system, and for biological homeostasis this means the dynamic maintenance of the internal environment within tolerable limits. Here is an example of biological homeostasis: under favorable climatic conditions, the reproducing females of the European lizard *Lacerta vivipara* will lay eggs. In high altitudes or high latitudes, the females will retain the eggs in the oviduct in order to maintain optimal temperatures for the development of the embryos by behavioral thermoregulation. This example has been used as a model for the study of the evolution of viviparity amongst lizards (Heulin et al. 1993; see the extended discussion in Pough et al. 2004). There is no reason why some homeostatic system should not be able to evolve from some other such system. Indeed, in his classic book on the synthesis of evolutionary theory, Mayr (1963, 61) invoked species-specific homeostatic mechanisms. The whole debate about the punctuated equilibrium theory of evolution (Gould 1982) centers on the issue of (homeo-)stasis versus change. But as with the application of natural kind terms, the relevance of the concept of homeostasis for species is more complex and maybe more controversial than for supraspecific taxa (a more complete discussion will therefore again have to be the subject of a future contribution). It depends, to some extent, as to how species are conceptualized (defined: Barton 1989), e.g., whether as open or as closed systems (Rieppel 1986).

In contrast, the relevance of homeostasis for supraspecific taxa is hardly controversial. The homeostatic mechanisms that keep supraspecific taxa afloat yet anchored in morphospace are the ones discussed above, which can be summarized under the heading of mechanisms of developmental integration (e.g., Alberch 1980). The striking efficacy of these mechanisms is perhaps best documented by the concept of 'forbidden morphologies' as it applies, for example, to the tetrapod limb (Stock and Bryant 1981). This concept of 'forbidden morphologies' explains the 'logic of monsters' (Alberch 1989), i.e., the fact that there is discreteness and order even among malformations that result from developmental disturbances. It is the genetic, epigenetic, and developmental homeostatic mechanisms which make it possible that species, as well as supraspecific taxa, can be 'identified and classified' (Alberch 1989, 21). Indeed, the interesting and important suggestion has been made that developmental modules themselves are homeostatic property cluster natural kinds (Wagner 2001).

Conclusions

If the above is correct, then the science of biological systematics is eminently inductive (or abductive). Species relationships that are expressed by grouping species in a hierarchy of higher taxa cannot be a matter of deduction (see Kluge 2003a, b, and Crother 2002, for dissenting views). As was noted above, Dupré (1981) recognized that the genealogical hierarchy is parasitic on some other relation of similarity such as that provided by morphology but that at the same time there is no reason to expect natural kinds to fulfill both these disjuncts (genealogy versus morphological or molecular 'facts'). This is the same juncture at which Hennig (1950, 26) admitted to the re-interpretation of the hierarchy based on 'idealistic morphology' as a genealogical hierarchy. The problem only is that the hierarchy obtained on the basis of morphology (or molecular data) is based on the membership relation, in contrast to the genealogical hierarchy which, in the way Hennig (1950) understood it, is based on the part – whole – relation (mereological inclusion: Rieppel 2003). These relations (membership versus part – whole) imply different ontological commitments (Sober 1984; Dupré1993; Boyd 1999; see Hull 1999, for a recent discussion). For Hennig (1950), the genealogical hierarchy is one of individuals that are part of larger individuals (the whole tree of life being the ultimate individual, some sort of 'superorganism': Wilson and Sober, 1989). Leaving the question of the ontological status of species aside [Hull 1999; Boyd 1999; see Hennig's (1966) concept of tokogenetic relations at the species level], Hennig's (1950, 1966) request that non-monophyletic groups must be replaced by monophyletic groups results in the insight that the hierarchy of higher taxa can be conceptualized as a hierarchy of natural kinds. A solution, then, to Hennig's (1950, 26) problem of the genealogical re-interpretation of the hierarchy of types based on morphological investigation obtains if this hierarchy of types is considered as stereotypical, i.e., a descriptive representation of a hierarchy of natural kinds whose extension needs to be 'filled in' by scientific theory construction. However, the hierarchy of kinds obtained on the basis of morphological investigation and parsimony will be one of property cluster natural kinds, and hence one of natural kinds with potentially fuzzy boundaries (Körner 1970; Putnam 1996). Hence the natural shiftiness of natural kind terms that was identified above (de Sousa 1984). Investigations into developmental homeostasis, developmental constraints, and the integration of developmental modules of morphology (Wagner 1989, 2001; Larsson 1998) ultimately establish the extension of the stereotypical hierarchy as a genealogical hierarchy, i.e., as a hierarchy of homeostatic property cluster natural kinds, with genealogy being one of the homeostatic mechanisms (Boyd 1999).

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