Natural Kinds in Evolution and Systematics: Metaphysical and Epistemological Considerations

Ingo Brigandt

Department of Philosophy
University of Alberta
2-40 Assiniboia Hall
Edmonton, AB T6G 2E7
Canada

Tel: +1 780-492-0623
Fax: +1 780-492-9160

Email: brigandt@ualberta.ca

Keywords:
natural kinds, species, taxa, homologues, analogues, induction, explanation

Abstract

Despite the traditional focus on metaphysical issues in discussions of natural kinds in biology, epistemological considerations are at least as important. By revisiting the debate as to whether taxa are kinds or individuals, I argue that both accounts are *metaphysically* compatible but one or the other approach can be pragmatically preferable depending on the *epistemic* context. Recent objections against construing species as homeostatic property cluster kinds are also addressed. The second part of the paper broadens the perspective by considering homologues as another example of natural kinds, comparing them with analogues as functionally defined kinds. Given that there are various types of natural kinds, I discuss the different theoretical purposes served by diverse kind concepts, suggesting that there is no clear-cut distinction between natural kinds and other kinds, such as functional kinds. Rather than attempting to offer a unique *metaphysical* account of ‘natural’ kind, a more fruitful approach consists in the *epistemological* study of how different natural kind *concepts* are employed in scientific reasoning.

Although most discussions of *natural kinds* in evolutionary biology and systematics focus on metaphysical issues (e.g., what is a natural kind, or which biological things are kinds), epistemological considerations are at least as important (e.g., what epistemic-theoretical aims are pursued by using various natural kinds concepts, or how well are they met using a certain way of grouping objects into a kind). In the case of biological taxa, most biologists and philosophers favor the idea that species are individuals rather than natural kinds. Yet recently some philosophers have interpreted species as natural kinds using a revised notion of ‘natural kind’ as homeostatic property cluster, which has also gained acceptance among a few biologists (Keller et al. 2003; Rieppel 2007). I clarify how the notion of natural kind can be applied in the case of species and higher taxa by answering some objections, in particular the idea that natural kinds cannot be subject to evolutionary change (Sections 1 and 2). At the same time, I argue that a species or a higher taxon can be construed *both* as an individual and a natural kind, i.e. both views are *metaphysically* compatible. Yet one conceptualization can be *pragmatically* preferable depending on the *epistemic* considerations that are in play in a certain scientific context. Taxa are best construed as natural kinds when they are viewed as taxonomic units, while it is preferable to view taxa as individuals when they are conceived of as units of evolutionary change.

While past discussions have focused on species and other taxa, the aim of this paper is to obtain a broader perspective on natural kinds in biology by considering further examples. Section 3 discusses homologues. While a higher taxon groups whole organisms, homology relates organismal parts by common ancestry. In addition to the analogy to higher taxa, homologues are like species units of phenotypic evolution. I argue that homologues as units of morphological change can in fact be considered natural kinds, yet this requires a specific way of applying the notion of a natural kind. This account will also shed some light on the relation between developmental and phylogenetic approaches to homology. Section 4 addresses functional kinds such as analogues. A common philosophical assumption is that functionally defined kinds are not natural kinds, as a function can be realized in different ways, so that functional kinds are structurally very heterogeneous and lack unity. However, not only clear-cut natural kinds (such as homologues) but also functionally defined kinds (such as analogues) can figure in important scientific generalizations, which points to an epistemic commonality.

The concluding section turns explicitly to epistemological issues. Given that the basic metaphysical notion of a natural kind is spelled out in different ways for the various kinds addressed, the different theoretical-epistemic purposes served by and explanatory advantages offered by different kind concepts are emphasized. I argue that there is no clear-cut distinction between natural kinds and other kinds (such as functional kinds). Rather than attempting to offer a unique *metaphysical* account of 'natural' kind, the more fruitful approach consists in the *epistemological* study of how and for what purposes various natural kind *concepts* are employed in scientific reasoning.

1. The homeostatic property cluster view of natural kinds

While species had originally been considered as classes or natural kinds, the view that species are individuals (SAI) was proposed in response to the serious problems facing a construal of species as kinds (Ghiselin 1974; Hull 1978). Most importantly, species are historical entities: a species originates, it persists across time at specific spatial locations, it can undergo substantial evolutionary change, and it can go extinct. The traditional notion of a natural kind is inadequate when applied to species as this notion was tied to kinds as found in physics and chemistry. The traditional account (used especially by metaphysicians and philosophers of language) construed a natural kind as a special type of class characterized by two features. (1) All members of a natural kind have the same characteristic properties, permitting universal generalizations, such as laws of nature (e.g., all oxygen atoms share physical properties and can undergo the same chemical reactions). (2) The identity and boundary of a natural kind is *metaphysically* determined by an essence; an object belongs to the kind in virtue of having this essential property. The essence is *epistemologically* fundamental in that it explains the characteristic properties of the kind (e.g., the essence of oxygen is its atomic structure, which explains all physical and chemical properties of oxygen). The first condition does not apply to species as there is substantial variation across the members of a species, and even a feature shared by all conspecifics at a time may be modified in evolution. In the case of the second condition, though it has never been part of the definition of an essence, an essence has typically been taken to be an *intrinsic* property of a kind member, as in the case of chemical structure. But no intrinsic property (= internal feature) of an organism—be it genotypic or phenotypic—can serve as the definition of its species (in contrast to merely diagnostic features), as other species members have or may evolve different features.

Yet the view that species and higher taxa are natural kinds has been revived (Boyd 1999; Griffiths 1999; Keller et al. 2003; Rieppel 2005b, 2006, 2007; Wilson 1999, 2005), using the view of natural kinds as *homeostatic property clusters* (HPC) proposed by Boyd (1991). This new philosophical notion of a natural kind was developed so as to do justice to natural kinds as they are studied in biology and other special sciences. It attempts to reconcile the fact that such kinds are typically heterogeneous and cannot be defined by necessary or sufficient conditions, with the observation that such categories are not formed in an arbitrary fashion and permit scientific generalizations and explanations.

The HPC view of natural kinds modifies both of the above conditions. (1) For any natural kind there is a cluster of properties that are correlated, typically by most of the kind members possessing most of these properties. None of the cluster properties has to be possessed by all kind members, so that the HPC view *permits variation* in the distribution of the properties that are characteristic of the kind, which is necessary for taxa to count as natural kinds. (2) These correlation of properties is brought about and maintained by causal processes (dubbed ‘homeostatic mechanisms’) in which the kind members figure. It is this set of homeostatic mechanisms that determines the identity of an HPC natural kind, i.e. specifies which objects are kind members, where vague boundaries are permitted. The kind is a ‘natural’ kind (rather than a nominal kind consisting of objects that are grouped together by mere human convention), as our grouping of entities into an HPC kind is rooted in objective features of nature. The causally grounded property correlation also makes possible the scientific generalizations and explanations in which the kind figures. Therefore, the homeostatic mechanisms play the same role as the ‘essence’ of a traditional kind (metaphysically determining the kind’s identity and epistemologically explaining its characteristic properties), yet the HPC view does not require that the kind is defined by is a *single* and *unchanging* essence rather than a complex property including a whole set of dynamic causal processes. To the extent that the kind has vague boundaries, among the kind members there may also be some variation in these homeostatic features, so that not every kind member need possess all of them to the same extent. Furthermore, in contrast to the tacit assumption (fitting chemical kinds) that an essence is an intrinsic property, the HPC view explicitly permits *extrinsic / relational properties* as part of the homeostatic mechanisms characterizing a natural kind. (For a more detailed philosophical account of the HPC construal of natural kinds see Wilson et al., in press.)

To illustrate this account briefly with examples, in the case of a higher taxon as a natural kind, the property cluster consists in character distributions, usually phenotypic (and genotypic) features shared by most species belonging to this taxon, i.e. synapomorphies. The fact that in each taxon member these characters tend to occur together and that each character is shared by most members is explained by common descent from a founding species, so that common descent is the causal process (‘homeostatic mechanism’) determining the identity and boundary of this higher taxon. Common ancestry is an *extrinsic* (= relational) property: being descended from a founding species is a property of a species (belonging to the taxon), but the species has this property not solely in virtue of its internal features, but due to its relation to another species. In the case of a species as a natural kind, the property cluster consists in shared phenotypic and genotypic features or a particular range of variation that several characters exhibit, which make the species a genetically and morphologically cohesive entity. The homeostatic mechanisms accounting for this are those described by some of the species concepts: gene flow and interbreeding, common descent, or ecological selection, all of which are relational properties and not just intrinsic to an organism that is a member of the species. For many species taxa several of these causal processes are relevant for maintaining the species’s coherence, so that the identity of a species as a kind is determined by a whole set of mechanisms that are causally intertwined. As a basic metaphysical account of natural kinds, the HPC view is not committed to specific homeostatic mechanisms (Wilson et al., in press). It is an *empirical* question what the relevant mechanisms are in the case of species taxa and the answer may vary from taxon to taxon (de Queiroz 1999); and there may be more than one answer, making room for pluralism about the species category. In sum, by permitting relational features such as common ancestry, the HPC view conforms to the fact that *history* is an important part of the identity conditions of taxa.[1]

---

[1] Ereshefsky (2007) argues against construing taxa as kinds, claiming that HPC kinds unlike individuals can be paraphyletic and even non-historical. However, this conflates the *empirical* question as to whether all taxa are monophyletic with the *metaphysical* question as to whether such taxa are kinds or individuals. Ereshefsky fallaciously concludes from the fact that *some* “*HPC kinds* need not be historical entities” that “HPC theory allows *taxa* to be nonhistorical entities” (p. 297; my emphasis). ‘HPC kind’ being a basic metaphysical category, some HPC kinds are historical and others are non-historical. In the special case of taxa, for empirical reasons taxa must be historical and probably exclusively monophyletic—also when viewed as HPC kinds. Similarly, being monophyletic is not part of the metaphysical category of ‘individual’, and some individuals (non-taxa) are not ‘monophyletic’.

Note that while the alternative SAI view does not explicitly invoke ‘essences’ (or homeostatic mechanisms), it is committed to there being some *determining* features that settle what makes some organisms (but not others) parts of a species and that determine the identity of this species-individual across time. These determining features may be unknown, though they are at least partially laid out by species definitions (Rieppel 2005b). Still, the position that species are individuals has to rely on features determining the identity of a species, viewing these features as specifying which organisms are parts of the species-individual, while a natural kind approach may view the *same* features as defining which organisms are members of the species-kind. In this sense the SAI position is committed to an ‘essence’ (or whatever term is used for the feature determining an entity’s identity) to the same extent the HPC view is; and in fact the label ‘essence’ has nothing to do with taxonomic essentialism.[2]

2. Species and higher taxa as individuals and as natural kinds

A clear advantage of the view that species are individuals stems from the fact that species are cohesive units that are able to undergo change. As I do not intend to deny this virtue of the SAI position, I focus on laying out why the HPC view can also accommodate this fact about taxa. Individuals are the kind of entities that have a spatio-temporal unity, whereas the members of traditional kinds (e.g. chemical kinds) are similar, yet spatially and causally unconnected objects.

---

[2] Keller et al. (2003) and Rieppel (2006) argue that SAI is committed to a version of essentialism (features that determine a taxon’s identity), which Rieppel calls ‘origin essentialism’ (taxon’s identity is determined by its origin). Ereshefsky (2007) objects that these authors conflate origin essentialism and (outdated) qualitative essentialism. However, pointing out that origin essentialism is a variety of *essentialism* does not conflate origin with *qualitative* essentialism. Ereshefsky is obviously inconsistent when both arguing that origin essentialism and qualitative essentialism are two distinct types of essentialism and that endorsing origin essentialism (as SAI does) is not endorsing essentialism. As proponents of the view that taxa are kinds do not endorse traditional qualitative essentialism but permit relational-historical essences, they endorse the same kind of essentialism as the SAI account.

This provides a relevant motivation for SAI, but has to be qualified. Barker and Wilson (unpubl.) make the useful distinction between integrative and response cohesion. An entity has *integrative cohesion* if its parts are spatially contiguous and there are strong causal connections between the parts so as to facilitate integration into a whole. A species taxon has only low integrative cohesion: the organisms belonging to a species can occupy remote locations and the causal interaction between conspecifics (interaction within the species-individual) is often no higher than interaction between such parts of the species-individual and other organisms and inanimate objects. In this respect a species taxon is unlike paradigmatic individuals—such as organisms—that have a high degree of integrative cohesion; and the HPC view can likewise capture this low degree of integration as it defines kind membership in terms of relational properties and causal connections to other species members (e.g. common ancestry, interbreeding). What species have to a high degree is *response cohesion*, i.e., the feature that the parts of the entity respond together (respond in the same way) to external causal influences. Response cohesion does not imply integrative cohesion: the parts of the entity can react in the same way even without interaction among them because of a common cause or because they face similar causes.[3] In the case of species, even organisms located at distinct places without any interaction can change in similar ways, as they are genetically and phenotypically similar and often encounter similar environmental conditions: response cohesion without integrative cohesion.

The notion of response cohesion is important because it is precisely the sense in which species behave as 'units' in evolution. The most significant motivation for the idea that species

---

[3] If the different persons living in a neighborhood communicate and interact to exert a social or political influence, the neighborhood manifests integrative cohesion. In contrast, in the case of a power outage, different persons in this neighborhood could respond in the same way (e.g., lighting candles, calling the electricity company). This can have an overall effect (e.g., the restoration of power), in which case the neighborhood displays response cohesion without any interaction among the various individuals (Barker and Wilson, unpubl.).

are individuals stems from the fact that individuals are the kind of entities that persist across time and can undergo change, changing as a cohesive unit. The fact that species evolve has often been viewed in conflict with the assumption that taxa are kinds—a legitimate objection given the outdated account of natural kinds. Kluge (2003) makes the same objection against the HPC view: "whatever is 'homeostatic' cannot, by definition, evolve" (p. 234). This is first a misconstrual of the HPC view, in that it takes the label 'homeostatic' too literally. 'Homeostatic mechanism' is a technical term that does not imply that the properties of a kind do not change or exhibit variation, rather, it refers to those causal processes that determine the boundary and integrity of the kind.

Kluge's objection is also not clear about the sense in which species evolve. Species are units and evolve *as a unit* in two related ways: (a) despite intraspecific variation, the different members of a species are phenotypically and genetically similar, relative to other species; (b) if evolutionary change occurs the species changes as a whole, i.e. the phenotypic and genotypic change obtains for most members of the species—response cohesion. At any point in time there are similarities across conspecifics ('homeostasis'), supported by mechanisms such as gene flow (one of the several features determining a taxon's identity on HPC accounts). If significant change occurs in some populations, this change is *transmitted* to other populations via gene flow (the homeostatic mechanism), resulting in the species changing as a unit. Thus, *some* homeostatic mechanisms (e.g. gene flow) can both generate unity/similarity at any point and account for why change obtains for the entity as a whole (response cohesion). The HPC view accounts for the way in which a species is a unit and changes *as a unit* if it changes. To explain why a certain change occurred, other considerations apart from the homeostatic mechanisms have to be adduced (mutation, selection)—the HPC view of *what a taxon is* does not pretend to account for why evolutionary change resulted. In general, many species concepts and definitions of higher taxa provide an account of the features that determine their boundaries and unity (phylogeny, gene flow, …). Assuming that such accounts are empirically adequate—conforming in particular to the fact that taxa evolve—the HPC view can simply take over these features in its account of what the 'homeostatic' mechanisms are.

A related objection against the HPC account was brought forward by Ereshefsky and Matthen (2005), who claim that as every natural kind account focuses on features shared by the members of the kind, it cannot account for variation within taxa, in particular stable polymorphisms. But the HPC view recognizes two sets of features: 1) a cluster of properties and 2) homeostatic mechanisms accounting for the properties' clustering. The account is committed to the features in set 2 being shared by most members of a kind (vague boundaries between biological kinds are permitted), because they determine which objects are part of the kind. Other features may show substantial variation: a higher taxon is defined by common ancestry from a particular species—any species belonging to the taxon must have this (extrinsic) property—yet this is consistent with as much character differences within this higher taxon as needed. Even the features in set 1 (that are part of cluster diagnostic of the kind) may be subject to variation: as such the HPC merely maintains that there is a *characteristic distribution and correlation* of these features. It may be that the distribution is such that a property is shared by all members, or it can be such that organisms that have character A_1 also tend to have A_2, while other organisms have B_1 (instead of A_1), which is correlated with B_2. This way the HPC view can cover sexual polymorphisms if A_1=male and B_1=female, and seasonal polymorphisms if A_1 refers to a particular season or life-history stage (Rieppel 2005b). What is shared are complex and conditional properties such as 'if female than B' or 'if larva then C'. Variation and polymorphisms may mislead taxonomists for some while, but these complex properties and correlations are discovered and clearly taken into account by researchers.

Ereshefsky and Matthen's (2005) main complaint about the HPC view is that it does not *explain* variation within taxa such as stable polymorphisms. I agree that explaining variation is important for biology, yet it is not a task for the HPC view or any other *account of what determines the unity and boundary of a taxon*. Take a species exhibiting sexual polymorphism. Organisms belong to this species in virtue of certain features H (including common ancestry); both males and females share H. The differences between males and females are of course due to *other* features (such as particular genes on sex chromosomes), which are not shared by both sexes. The HPC account—specifying that an individual belongs to this species in virtue of possessing H—does not and need not explain such differences among species members, but it can feed into such an account. The set of homeostatic mechanisms H may include genetic and developmental features shared within the species. The male phenotype results from H in combination with male sex genes (H+A), the female phenotype results from H together with other genes (H+B). Thus, differences among the members of a taxon are explained by a combination of causal factors shared by all members (that the HPC view may use to define the taxon) and factors specific to a subset of the taxon members. In general, one classification or kind concept (e.g. classifying organisms into species or the concept *Gallus gallus*) cannot be expected to capture all generalizations in which organisms figure. Different generalizations may require different kind concepts (e.g. ‘male organism’ and ‘female organism’, yielding also the subkind ‘male chicken’), and an organism usually belongs to several kinds.

So far I have focused on species as *evolutionary* units, acknowledging that construing species as individuals fits nicely with species being units of evolutionary change, while arguing that species can also be conceived as HPC natural kinds. Now I move to species and higher taxa as *taxonomic* units. Needless to say, taxonomy is in the business of grouping organisms into species and organisms/species into higher taxa according to their phylogenetically grounded character similarities and differences. A phylogenetic classification yields descriptions that at the same time cover *large* taxa and assign *many* correlated features to the organisms of these taxa. Apart from providing generalizations of the features of organisms, a phylogenetic classification also ties into the evolutionary study of the phylogeny of taxa and their characters. The view that taxa are natural kinds (or classes) having organisms as its members fits smoothly with the fact that taxa encompass organisms sharing salient biological properties. Still, also the rival view that taxa are individuals can accommodate this, once it is pointed out that a taxon as an individual has organisms as its parts which can be compared and classified and share many properties.

Apart from the issue as to which *metaphysical* category taxa belong to, an important virtue of some discussions developing the HPC view has been to address *epistemological* issues in biology. While it is not committed to natural kinds being governed by genuine laws, the HPC view stems from the idea that any adequate scientific account of a particular natural kind permits important *inferences* (induction) and *explanations* (Boyd 1991; Griffiths 1999). Boyd (1999) offers a particularly explicit discussion based on the notion of ‘accommodation’. The starting point is that biologists have various epistemic aims (inductive and explanatory demands), e.g., putting forward generalizations about the phenotypic properties of taxa, or explaining speciation. Boyd construes a grouping of objects (a kind) as ‘natural’ in case this group of objects shares certain properties that fulfill the inductive and explanatory aims, i.e. accommodate the epistemic demands. An account of the natural kind (in particular the specification of the homeostatic mechanism determining the kind’s identity) typically answers to fairly demanding theoretical issues and for this reason becomes available only based on empirical research, sometimes long after the emergence of the idea that there is a natural kind and the introduction of the word naming it. Consistent with this, Rieppel (2005b, 2006, 2007) argues that epistemic considerations influence the reference of taxonomic terms.

Several epistemic aims may attach to one and the same natural kind, and a beneficial feature of the HPC view is that it can capture and relate different epistemic endeavors, by showing how different scientific approaches capture different aspects of an overall complex phenomenon. A natural kind is characterized by a correlation of properties, which permits *descriptions and inductions*. In addition to this, some of the features shared by members of the kind are more basic in that they form the *causal* basis for the correlation of the other features. These features making up the homeostatic mechanisms support *explanations*. For instance, a species shares many properties, to which species concepts focusing on *diagnostic* and operational properties may appeal (e.g. the morphological species concept, the phenetic species concept, the apomorphy species concept); and a species has a unique evolutionary fate (as pointed out by the evolutionary species concept). Other species concepts may focus on *explaining* some of these facts about species, such as explaining shared characters within species and character differences across species by phylogenetic branching, gene flow, or ecological selection. In addition to phenotypic similarity, the biological species concept and the recognition species concept explain why species have a unique evolutionary fate, and they tie into explanations of speciation.

The HPC approach views these different descriptive and explanatory interests (epistemic aims) as compatible. While one scientific account (e.g. one species concept) represents only some properties of a kind (because those are sufficient to accommodate the specific epistemic interests of a group of biologists), the HPC view highlights how many more properties tied to a kind are metaphysically related. By for instance laying out the causal relations among shared phenotypic features, cohesion mechanisms, evolutionary unity, the HPC approach also provides resources for showing how different scientific representations, concepts, and models are epistemically related or can be theoretically integrated. In the case of higher taxa as another example, shared features serve as diagnostic characters. The occurrence of such character distributions is explained by causal mechanisms such as common ancestry and the operation of developmental constraints. Rieppel and Kearney (2007) argue that a deeper *explanatory-theoretical* understanding of the causal basis of character evolution (including accounts of developmental constraints, modularity, and ontogenetic repatterning) would improve the *descriptive* practice of taxonomy, by providing insights into which characters are actually independent of each other and how informative various characters are for setting up phylogenies.

My overall conclusion on the individuals vs. natural kinds debate is that both positions are *metaphysically* consistent. I do not see any reason why an object could not be construed as an individual and a natural kind *at the same time*, and take biological taxa—both species and higher taxa—to be such objects (as already suggested by Dupré 1993). One metaphysical account can be translated into the other and *vice versa* (see LaPorte 2004 for a detailed discussion): An organism is ‘a part of a species-individual’ on SAI, while the HPC view has to conceptualize this organism as ‘a member of a species-natural-kind’, and translate any talk about organisms accordingly (and *vice versa* for SAI). An individual changes in the straightforward sense that different time slices of this individual have different properties. Yet a species-natural-kind can also be conceived of as changing if some of the members of the kind have different properties at different times.[4] A natural kind has pre-given members that make up the kind in the first place. These are individual organisms in the case of taxa—fundamental biological units to which descriptions and explanations apply. While an individual does not have pre-given parts, the SAI

---

[4] Stemming from Ghiselin (1974) and Hull (1987), a common objection against viewing taxa as kinds is the idea that unlike individuals, kinds are spatiotemporally unrestricted (Ereshefsky 2007). On my account, ‘species-individual A is spatially unrestricted’ has to be translated by a kind approach as ‘the space occupied by the members of species-kind A is unrestricted’. If the putative objection is that the *actual* space taken up by a species-individual is restricted, so is the space taken up by the members of the corresponding species-kind. If instead the objection is construed as the idea that it is *possible* for members of a species-kind to occupy spatial locations far beyond the ones they actually occupy, the same applies for the species-individual. E.g., if the boundary of a taxon-individual / taxon-kind is determined by monophyly, taxon parts/members can possibly occupy any position of the universe insofar as it is empirically possible to reach that position without breaking monophyly.

approach is not debarred from explaining that any species-individual (and higher-taxon-individual) has organisms as central parts—parts that share properties so that generalizations apply to them. Both the HPC and the SAI view agree in endorsing some sort of realism about taxa, at least species taxa. Natural kinds are assemblies of objects that are grouped according to properties that actually exist in nature, so that the boundary and unity of a natural kind are not conventional. An individual likewise has a non-arbitrary boundary and distinctive unity across time. Monophyly is what determines the boundaries of higher taxa, and in the case of species there are several properties (common descent, gene flow, ecological selection) that are relevant for species cohesion. An HPC approach views these features as the homeostatic mechanisms determining membership in a taxon-kind, while SAI construes such features as determining the unity of the taxon-individual across space and time.

Although *metaphysically* both approaches are fully compatible, there may be *pragmatic* reasons to favor one over the other in a certain *epistemic* context. In evolutionary contexts where species (and sometimes higher taxa) are viewed as *evolutionary* units that originate, undergo change, and go extinct, they are best viewed as individuals. As explained above, natural kinds can be conceptualized as changing, yet translating from individual talk to kind talk results in a less natural way of speaking in these contexts. In taxonomic contexts, where species and higher taxa are viewed as *taxonomic* units consisting of organisms sharing many biologically important characters, it is more natural to speak of taxa as natural kinds (Dupré 1999). This in line with Boyd’s (1999) suggestion that “by seeing similarities between the inductive and explanatory roles played by reference to natural kinds, on the one hand, and by reference to individuals, on the other hand, we can see why the distinction between natural kinds and (natural) individuals is, in an important way, merely pragmatic. … A failure to be able to recognize various stages in the maturation of an organism *as stages of the same organism* [individual] would undermine induction and explanation in biology just as much as a failure to deploy accommodated schemes of classification for the organisms themselves" (p. 163).[5]

3. Homologues as natural kinds

Discussions about biological kinds have focused on species and other taxa. However, the aim of this paper is to arrive at a broader perspective on natural kinds in biology, so that it is vital to consider other examples, and to discuss what different types of 'homeostatic mechanisms' can determine the identity of kinds and what various epistemic aims guide the study of kinds. In this section I turn to homologues. Homologues share many features across taxa; and phylogenetically based similarities are used to group structures in different organisms/species (token homologues) together as homologues or structures of the same type (homologies across species). This *taxonomic* aspect of homology (stressed by taxic approaches to homology) clearly fits the conception that homologues are kinds, just like higher taxa are naturally seen as kinds grouping species according to their phyletically based similarities. Furthermore, a homologue as a part of the body has a morphological and *developmental* influence (Müller 2003; Love and Raff 2006), and these causal properties of homologues provide a further reason to view them as natural

---

[5] While the individualism vs. kinds debate is an issue about species *taxa*, species *pluralism* is a question about species *categories* or *concepts*. I endorse a plurality of species concepts (combined with a generic species concept encompassing all particular species concepts similar to de Queiroz 1999), but in addition to metaphysical arguments I emphasize that there are also epistemological reasons (Brigandt 2003). The metaphysical basis of pluralism is that there are several mechanisms generating species cohesion which sometimes do not align and delineate different species taxa, so that different species concepts can focus on one or the other mechanism. But there are also different legitimate scientific tasks or epistemic aims pursued (taxonomic, evolutionary, ecological tasks; explanatory, operational aims); and a particular species concept may be better suited than others for such an epistemic task. Some species concepts (used in some epistemic contexts) focus on species as evolutionary units, while others (used in other contexts) focus on species as taxonomic units, which in line with the above means that species are better viewed as individuals or kinds depending on the epistemic context and species concept employed.

kinds—in fact, the question is which possible parts of a body are natural units in that they have a distinct developmental role and can function as independent taxonomic characters. Previous discussions and explicit defenses of the idea that homologues are natural kinds were given by Wagner (1996, 2001) and Rieppel (2005a), appealing to the HPC view. What I want to focus on here is homologues as units of *evolutionary* transformation (as emphasized by transformational approaches to homology), laying out how the HPC view and the properties defining a natural kind have to be understood in this case to construe homologues as units of change, in analogy to regarding evolving species as kinds.

An important starting point is the distinction between characters and character states. A homologue is a *character* in different species even if it takes on different *character states* in these species. For a homologue to function as a unit of evolutionary transformation, structures in different species can be homologous even if these structures are quite dissimilar. If a homologue is conceptualized as an individual—which is possible in line with the above account of the metaphysical status of taxa—then this homologue-individual has as its mereological parts various token homologues (parts of single organisms), which are united as parts of a transformation lineage (or actually several lineages leading from an ancestral structure to any of its descendant structures). Correspondingly, a homologue construed as a natural kind is a class containing various token homologues as its members. Now, previous discussions, in particular *developmental approaches to homology*, have stressed features shared by token homologues. However, while token homologues are often similar (of the same state) in closely related species, structures in unrelated species can be the same character even if they are in very *different* character states. How to reconcile this with the idea that a natural kind is defined by certain features (homeostatic mechanisms) shared by all or at least most kind members? The answer is that among the various developmental and morphological properties of a particular structure in an individual, only *some* determine this structure being homologous to structures in other organisms. Certain features of a developmental process may determine the identity of a character and occur in every instance of this character in different organisms and species. Yet this character takes on different states in different species which is due to other developmental features differing between these species. This is in analogy (or homology) to the above point that there are certain features that determine the identity of a species or higher taxon (descent from a founder group, gene flow) and are possessed by every member of this taxon, while the variation within the taxon is due other biological properties that vary among taxon members.

Which developmental-morphological properties of a structure determine its identity as a homologue and which do not (and thus can vary across species) has to be teased apart by detailed comparative developmental studies. For instance, Wagner (1989) suggested that homologues are characterized by shared developmental constraints. Whatever developmental features are shared by structures when they are governed by the same ‘developmental constraints’, Wagner was clear about the fact that the sharing of such constraints is consistent with a homologue developing differently in different species (Wagner and Misof 1993), so that while some developmental features are shared by homologues, others are not. Wagner (2007) recently suggested based on concrete cases that there are gene regularity networks which as character identity networks (ChINs) are present in any instance of a *character* across species, whereas other genes that are not part of the ChIN vary so as to lead to different character *states* in different species. Thus, the biological properties determining the identity of a homologue as a natural kind have a dual role. They are reliably inherited across generations and hard to modify (‘constrained’), resulting in the same character being present across individuals and species (unless the character merges with others, splits into two, or is simply lost). At the same time, these developmental properties determining character identity provide the very basis for this homologue undergoing evolutionary change by permitting other developmental properties to change without resulting in the loss of this character.

Section 1 highlighted the idea that the identity of an HPC natural kind is not necessarily constituted by intrinsic properties, i.e., the homeostatic mechanisms specifying what the kind's members are can include *extrinsic or relational properties*. This is relevant in the present context because given that a homologue can take on various character states and thereby vary in its internal structure across species, the identity of a homologue may not be determined solely by features *internal* to this structure. My suggestion is that a structure is a homologue as a unit of phenotypic evolution to the extent that it is distinct from *other* such units, i.e., to the extent that the structure can undergo phenotypic change largely *independently of other homologues* (Brigandt 2007; see also Wagner 1996; Laubichler 2000). Thus, an important aspect of the developmental properties determining the identity of a homologue is the way in which this structure is partially *developmentally dissociated* from other structures so as result in distinct (semi-autonomous) units of evolutionary change. The growing literature on modularity (Bolker 2000; Rieppel 2005a; Schlosser and Wagner 2004; von Dassow and Munro 1999; Winther 2001) offers a partial explanation of how structures that are developmentally and functionally related can be sufficiently dissociated so as to permit morphological change. Furthermore, homologues exist on several levels of organization (homology among genes, developmental processes, adult morphological structures, behavioral patterns); and homology on different levels can be dissociated, e.g., a homologous structure can develop by different developmental processes and by the action of non-homologous genes. As a result, accounting for the identity of a homologue involves the question of how this homologue can evolve fairly independently from homologues on other levels of organization, despite the close causal relation between entities on different levels such as genes, developmental processes, and morphological structures (Brigandt 2006).

In sum, different instances of a homologue in different species may share a host of internal structural properties, which is important for systematics. Yet despite the focus on shared features in many discussions of natural kinds, different instances of a homologue may differ in their character states. The 'homeostatic mechanisms' determining the identity of a homologue as a natural kind are shared by all instances of a homologue, yet these defining developmental features are much lower in number than the many similarities of homologous structures in closely related species and furthermore may include relational properties. This specifies why the structure is a 'natural' kind as a natural unit partially dissociated from other parts of the body, so that it can function as a unit of phenotypic transformation by changing in its *internal* structure, while its *relation* to (and dissociation from) other homologues remains largely stable.

My earlier work attempted to bridge the gap between *developmental* and *phylogenetic* accounts of homology (Brigandt 2007). Here I merely sketch why I view both approaches as compatible and how they are related, adding how the HPC view of natural kinds contributes to this. Both approaches simply address different aspects and temporal stages of one complex phenomenon. Developmental approaches focus on the developmental-morphological features that are the basis of structures being dissociated so that they can evolve as distinct characters. This developmentally based potential for evolution manifests itself in certain phylogenetic patterns, i.e., distributions of character states. Phylogenetic (taxic) approaches to homology simply focus on the phylogenetic manifestation of the potential for evolution in a character-by-character fashion. The HPC view contributes in clarifying the relation between both accounts as follows. A developmental account focuses on the *homeostatic mechanisms* that form the causal basis of homologues as natural kinds. These developmental features (together with other factors such as phylogenetic branching and causes of character change such as selection) are the basis of the resulting patterns of character state distributions and synapomorphies among extant species—making up the *cluster of properties* and correlations diagnostic of an HPC natural kind. Thus, taxic approaches focus on a homologue as a natural kind in that there is a large cluster of shared character *states* (at least among closely related species); while developmental approaches focus on a homologue as a natural kind in that there are features that determine the identity of this *character* as a natural unit of evolutionary change independent of other such units. While pursuing quite distinct *epistemic* tasks (classifying species vs. explaining the developmental basis of evolution), both approaches are seen as compatible once it is clarified how they address different aspects of one overall process (the phenotypic product of evolution and the developmental basis of evolution).

4. Analogues and other functional kinds

Apart from kinds defined in terms of structure and/or phylogeny, there are kinds defined in terms of function features, so that an account sensitive to the different kinds of biological kinds has to consider functionally defined kinds such as analogues and ecological kinds. Some philosophers assume that a functional kind is not a natural kind (and instead a set of several natural kinds), on the grounds that a function can be realized by different structural means, so that a functional kind is structurally heterogeneous, in contrast to the traditional vision that a natural kind is defined by a unifying structural feature. However, I argue that a more nuanced picture is needed, as functional kinds can figure in important scientific generalizations and explanations, thereby possessing an epistemic feature that is also a hallmark of natural kinds.

Ghiselin (1997, 2002) views *analogues* as more fundamental than homologues, based on the idea that homologues are individuals to which no laws apply, whereas analogues form classes, whose members are united by laws of nature. To some extent, Ghiselin has it backwards (Griffiths 1994, 1996, 1999). Character individuation by homology is so important for any comparative endeavor in biology precisely because homologues share so many properties, be it internal features (morphological, developmental, physiological), be it relational features (relation to other structures). The closer related the species compared are, the larger the number of properties shared, permitting generalizations across species. These are not laws, but character individuation by homology provides the scheme of individuation that permits the generalizations with the largest scope and accuracy. Research on model organisms is predicated on the idea that findings about a model species permit an inference to the corresponding structures and systems in other species—an inductive inference that is fallible, yet reliable. Due to the correlation of properties in homologues, knowing that an organism has feature A (say mammary glands) warrants the conclusion that it also has feature B (hair). The possibility of these generalization/inferences can be explained based on the fact that homologues are individuated in terms of common descent and structural features (developmental constraints), so that this ties also into explanations in phylogeny, evolution, and development. These facts have been the reason for philosophers to view homologues as natural kinds—kinds that share many scientifically important properties apart from the properties that were used to pick out the kind.

Analogues, in contrast, share significantly less properties than homologues because they are defined in terms of some function. Functional kinds are what philosophers call *multiply realizable*: there are many different possible physical systems (realizers) that perform the function. E.g., money is a functionally defined category from economics; and it can be realized by such different physical systems as metal (using gold as a currency), paper (bills), electrical states (electronic accounts and transactions)—which have hardly any material properties in common apart from the ones any physical entity possesses. In the case of functionally defined kinds in biology such as analogues, it is well known that analogues can be structurally extremely diverse, as the same adaptive problem can be solved in many different ways (e.g., digestive systems and locomotive systems are very diverse). Being analogues, bird wings and insect wings share a fairly low amount of morphological and developmental properties. To be sure, bird wings and bat wings share significantly more properties, but this is not because of them being analogues (wings as including also insect wings), but because of them being homologues (tetrapod forelimbs). The same applies for ecological categories as functional kinds, e.g., fresh-water predators can achieve their life-style in very different ways.

Ghiselin (2002), in contrast, maintains that the same laws apply not only to biological structures having the same function, but any physical system performing the function, e.g. "the wing of a pterosaur, a dragonfly, an airplane, and any other such component" (p. 288). Mechanical laws do apply to these structures, yet they also apply to most physical systems. The real issue (which Ghiselin misses) is whether there are many principles and properties that apply to the instances of a kind but not to other objects. Needless to say, animal wings and aircraft wings are totally different in their internal structure, and even different animal taxa differ substantially in how they morphologically and physiologically achieve wing movement. Even regarding the way in which different wings permit uplift, the similarities are of a modest degree. To account for how a particular wing permits flight, the laws of physics have to be applied in a concrete model.[6] But *different models* are needed to understand different kinds of wings. For instance, modeling insect wing uplift involves non-linear effects resulting from the wing rapidly changing its orientation towards the direction of relative air movement, and the fact that insect wings are not rigid airfoils but change their three-dimensional shape during flight—both factors do not apply for aircraft wings. In sum, while homologues share a host of properties beyond those used in the definition (common ancestry), analogues that are multiply realizable like other

---

[6] A law that is applied to one range of systems can be applied to many other kinds of systems. The flipside of the universality of laws is that for a particular system, several laws have to be combined in a system-specific manner.

functionally defined kinds share significantly less properties—a fact that holds independently of whether one views each as a natural kind or an individual, or uses a particular construal of laws. Contra Ghiselin, homologues seem to be much more like natural kinds than analogues do.

However, while the members of a kind defined in terms of phylogeny and/or structure (such as homologues) may share more properties than members of a kind defined in terms of function (such as analogues), functional kinds are nonetheless scientifically relevant and figure in certain generalizations. In line with my above remark, Griffiths (1999) acknowledges that there are indefinitely many ways to construct instances of money (so that different instances hardly share any internal structure), yet he points out that the concept of money is a central theoretical notion of economics and figures in generalizations of this field. E.g., there are principles as to how inflation results from an increase in the amount of money being present in an economy; and they are general precisely because they apply no matter in which ways money happens to be physically realized in a particular economy. What enables these generalizations is that money exhibits stable *relations* with other economic entities, such as exchange of goods and other values, the preferences of economic subjects, and economic development. Griffiths conceives of money as an HPC kind defined by a relational 'essence', and views as one of the virtues of the HPC approach that it includes theoretically important kinds of the special sciences as natural kinds. In a similar vein, Boyd (1999) construes social kinds as natural kinds to the extent that they exhibit stable relations (a social role maintained by social mechanisms) so as to meet some of the inductive and explanatory tasks of the social sciences.

In my view, the same applies to functionally or relationally defined kinds in biology, such as some physiological, ecological and behavioral kinds. Different structures that are analogous (*different members of the kind*) may not share many internal properties, but what matters is rather the functional relation between a particular analogue and other entities (*a kind member and* *members of other kinds*). Likewise in the case of ecological categories: different predators may not have much in common and hunt and feed in various ways, yet predators exhibit certain relations with their prey species so as to permit ecological generalizations about predator-prey interaction. Thus, while the amount of properties shared among members of a functionally defined kind may be lower than in the case of more paradigmatic natural kinds in biology (homologues, taxa), what is more relevant—than the sheer number of properties—is whether the properties shared and the generalizations in which the kind figures are *scientifically important* for the field under consideration. Boyd's (1999) notion of 'accommodation' is yet relevant again: Boyd starts out with the inferential and explanatory demands of a scientific field, and given this construes a natural kind as a kind that possesses properties that exist in nature and accommodate (some of) these epistemic demands, so that an assessment of the significance and 'naturalness' of a certain kind has to among other things to pay attention to the relevant *epistemic* demands.

5. Epistemological issues and the limits of purely metaphysical accounts

The HPC account maintains that a natural kind is characterized by a cluster of correlated properties, and that the metaphysical identity of the kind is determined by a set of homeostatic mechanisms, which form the causal basis for the correlation of the former properties. An HPC kind is a natural kind differing from an arbitrary grouping of objects by a merely conventional definition, as there are many more properties shared by most members of an HPC kind than the homeostatic mechanism used to define the kind. The existing correlation of properties can be used for the purposes of scientific induction, and the presence of causal features among them (e.g. homeostatic mechanisms) forms the basis of explanations. This is a very basic metaphysical view of what a natural kind is, and can be applied to different kinds in different ways.

The above discussion featured *several types* of natural kinds, and for each such type there are *different homeostatic mechanisms* specifying the identity of the kind. A higher taxon is defined by common ancestry, and possibly also by the operation of developmental constraints specific to that taxon, which together with common ancestry account for the character similarities among taxon members. A species can be characterized by various cohesion mechanisms (accounting for its unity in evolution), including common ancestry, gene flow, ecological selection, and developmental mechanisms (accounting for phenotypic unity, life-histories, or stable polymorphisms). This shows that for many natural kinds in biology, its boundary is not defined by a single feature, but by a whole set of causally interdependent processes, permitting even variation in the very features determining the kind's metaphysical identity. There are cases where one species taxon as a natural kind may be characterized by a homeostatic mechanism (e.g. interbreeding) that does not obtain for another species as a further natural kind (e.g. an asexual species). A homologue as a natural kind is constituted by certain developmental-morphological features (e.g. developmental constraints), which form the material basis for this homologue serving as a unit of phenotypic transformation. While the philosophical tradition has often viewed the identity of many objects being determined by intrinsic properties, we saw that the above types of natural kinds are defined at least in part by extrinsic and *relational properties* (which the HPC view explicitly permits). I take it that it is quite typical for kinds in biology that they are (partially) characterized by extrinsic properties.[7]

Thus, the HPC view of natural kinds is quite flexible and can be applied to many different types of natural kinds. The flipside of this is that the very claim *that* a collection of objects forms an HPC natural kind is relatively weak and as such not informative. The real question is *how and*

---

[7] E.g., a gene is a particular stretch of DNA, yet what makes this DNA segment a gene is its causal ability to code for a functional product, which also depends on DNA elements external to this gene and on non-genetic factors (a gene can turn into a pseudogene because of changes external to it). Being a gene is a property of a DNA segment, but an extrinsic one (holding in part due to features external to the bearer of the property).

for what reason these objects form an HPC kind; in particular, what the particular properties that are fairly reliably correlated are, and what the specific homeostatic mechanisms forming the causal basis for this correlation and the unity of the kind are. Knowing about these concrete features characterizing a particular natural kind permits scientific inferences and explanations—what Boyd (1999) calls 'accommodation' of scientific demands. The very *metaphysical* fact that something is a natural kind implies that there are properties that (if known) can be used for the purposes of scientific induction and explanation, yet such *epistemic* aims are actually met only to the extent to which there is a natural kind *concept* that embodies knowledge about the scientifically relevant features of the kind.[8]

This shows both that the metaphysical distinction between natural kinds and other kinds is vague and that epistemological considerations are vital when discussing various kinds. The traditional idea is that natural kinds are scientifically important because they exhibit fundamental properties supporting explanations. The HPC view does not assume that natural kinds can be theoretically important only if they figure in universal laws, so as to capture how kinds figure in theorizing in biology and other special sciences. As a result, there is no clear-cut criterion as to how many properties have to be correlated to which extent (and which causal features a homeostatic mechanism must have) that would determine whether a kind is an HPC natural kind or a non-natural kind. Apart from making the boundary between natural and other kinds a matter of degree, the real issue is the extent to which the inferences and explanations supported by the known properties of the kind are scientifically important. This involves the *epistemological* study of what the various inferential and explanatory aims of different scientific subdisciplines are,

---

[8] The HPC view acknowledges that such an account/concept of the natural kind, in particular its homeostatic mechanisms basis, may become available not until substantial empirical discoveries are made, long after the introduction of the term denoting the putative natural kind.

how they relate to each other, and how they are or can be met by scientific representations and kind concepts.

For instance, Boyd (1999) and Griffiths (1999) argue that social kinds and other kinds used in the special sciences can be natural kinds, and their examples make this point not by counting how many properties are correlated in such a kind or by assessing to which extent the generalizations they figure in count as laws, but by pointing out that the kinds support explanations that happen to be theoretically important given the scientific aims of the particular fields. Similarly, I acknowledged in the previous section that the individuation of structures in terms of analogy or function is legitimate as it meets *some* theoretical demands in biology, so that functional kinds can qualify as natural kinds. (This holds even if character individuation in terms of homology may in some contexts be more important than in terms of analogy given that homology provides one fundamental individuation scheme that contributes to meeting many *other* theoretical aims, and is used even in contexts where also functionally defined kinds are important).[9] As a negative example, take Machery's (2005) discussion of concepts in psychology. His legitimate point is that what psychologists call concepts consists actually of several different kinds of cognitive structures (prototypes, exemplars, …), all of which underlie some conceptual performances, so that debates among psychologists on 'concepts are prototypes' vs. 'concepts are exemplars' are misguided. Machery's conclusion is that the notion

---

[9] Okasha (2002) recognizes that on the traditional picture, a natural kind's essence has two roles: (1) determining the kind's identity, (2) causally explaining the kind's characteristic properties. While essences have often been construed as intrinsic properties, Okasha argues (in line with my account) that the traditional account can be revised by permitting relational essences. However, he maintains that in this case essences cannot play the putative second role, based on the assumption that only intrinsic properties can underwrite generalizations and explanations. My discussion shows that he is wrong on that count. The causal effect of many biological kinds (e.g. genes producing RNAs and polypeptides) depends on their context and relations to other entities. Successful explanations in ecology, physiology, economics and other disciplines routinely invoke extrinsic factors and stable relations among entities.

of ‘concept’ is not as important for psychology, and should be replaced in favor of more discriminating notions (such as ‘prototype’, ‘exemplar’). This is an interesting epistemological tenet about the *scientific* relevance of the psychological notion of a ‘concept’, to be debated in these terms; yet Machery attempts to establish this *epistemological* conclusion via a *metaphysical* detour, by trying to lay out a metaphysical definition of what a natural kind is and to show that concepts are not a natural kind (as consisting of distinct subkinds).

In my view, the question as to whether or not a scientific kind is theoretically important cannot be conducted in terms of whether it is a natural kind or another kind. Rather than attempting to offer a unique *metaphysical* account of ‘natural’ kind, the more fruitful approach consists in the *epistemological* study of how and with which success different natural kind *concepts* (and other concepts) are employed in scientific reasoning. Rieppel (2005b, 2006, 2007) discusses how theoretical considerations are relevant for how taxonomic terms (conceived as natural kind terms) are used, and how epistemic issues influence the reference and semantics of such terms. The above discussion of various biological kinds pointed to different epistemic aims. Some kind concepts support mere descriptions (induction, inference, generalization), other concepts support causal-mechanistic explanations. Some species concepts serve only taxonomic descriptions and classifications, other species concepts support evolutionary explanations. Some meet several such biological demands once combined with other concepts or items of knowledge. To cite just one among several examples, the biological species concept accounts for phenotypic unity within a species (given that the phenotypic expression of genes shared due to gene flow is taken into account), it accounts for some cases of speciation (once biogeographical considerations are added), and it explains how a species can undergo evolutionary change. A developmental homology concept accounts for the behavior of homologues in development, but also for their evolutionary role (by specifying how modularity and developmental dissociation permit different homologues to change in evolution as independent units, once other causal mechanisms such as natural selection effect change), which ties into phylogenetic character distributions relevant for systematics (Rieppel and Kearney 2007).

While a kind concept abstracts away from many features of reality and is not able to serve all scientific purposes, the concept may very well succeed in meeting some epistemic aims, so that it is important to get clear about which theoretical-epistemic purposes a natural kind concept is meant to serve (Love, this issue). In some cases, different such epistemic aims are compatible and can be jointly met by an integrated model or account of the kind, and the HPC view of kinds contributes to this by pointing out that many properties can be tied to a single biological kind and exhibit complex relations. Even if the features used to define an HPC kind result in this kind having a vague boundary, this is legitimate as long as the features support important scientific generalizations and explanations. The upshot of my discussion for the individualism vs. kinds debate is that the relevant question is not so much into which metaphysical category species and higher taxa fall, but how biological accounts of taxa (such as species concepts) underwrite classifications and generalizations, shed light on the unity of taxa across time, and permit explaining their ability to undergo change as a unit—all of which are epistemic issues.

Acknowledgements

I thank Francisco Vergara-Silva and Rasmus Winther for the invitation to contribute to this special issue. I am indebted to Matt Barker, Joseph LaPorte, Alan Love, Rob Wilson, and Rasmus Winther for helpful comments on earlier versions of this paper. The work on this essay was funded with an Izaak Walton Killam Memorial Postdoctoral Fellowship by the Killam Trusts of Canada, and with a Standard Research Grant by the Social Sciences and Humanities Research Council of Canada.

References

Barker MJ, Wilson RA (unpubl.) Flowing genes and cohesive species. Manuscript under review

Bolker J (2000) Modularity and why it matters to evo-devo. American Zoologist 40:770-776.

Boyd R (1991) Realism, anti-foundationalism and the enthusiasm for natural kinds. Philosophical Studies 61:127–148

Boyd R (1999) Homeostasis, species, and higher taxa. In Wilson RA (ed) Species: new interdisciplinary essays. MIT Press, Cambridge, MA, pp141–185

Brigandt I (2003) Species pluralism does not imply species eliminativism. Philosophy of Science 70:1305–1316

Brigandt I (2006) Homology and heterochrony: the evolutionary embryologist Gavin Rylands de Beer (1899–1972). Journal of Experimental Zoology (Molecular and Developmental Evolution) 306B:317–328

Brigandt I (2007) Typology now: homology and developmental constraints explain evolvability. Biology and Philosophy 22:709–725

de Queiroz K (1999) The general lineage concept of species and the defining properties of the species category. In Wilson RA (ed) Species: new interdisciplinary essays. MIT Press, Cambridge, MA, pp49–89

Dupré J (1993) The disorder of things: metaphysical foundations of the disunity of science. Harvard University Press, Cambridge, MA

Dupré J (1999) On the impossibility of a monistic account of species. In Wilson RA (ed) Species: new interdisciplinary essays. MIT Press, Cambridge, MA, pp3–22

Ereshefsky M (2007) Foundational issues concerning taxa and taxon names. Systematic Biology 56:295–301

Ereshefsky M, Mohan M (2005) Taxonomy, polymorphism, and history: an introduction to population structure theory. Philosophy of Science 72:1–21

Ghiselin MT (1974) A radical solution to the species problem. Systematic Zoology 23:536–544

Ghiselin MT (1997) Metaphysics and the origin of species. State University of New York Press, Albany

Ghiselin MT (2002) An autobiographical anatomy. History and Philosophy of the Life Sciences 24:285–291

Griffiths PE (1994) Cladistic classification and functional explanation. Philosophy of Science 61:206–227

Griffiths PE (1996) The historical turn in the study of adaptation. British Journal for the Philosophy of Science 47:511–532

Griffiths PE (1999) Squaring the circle: natural kinds with historical essences. In Wilson RA (ed) Species: new interdisciplinary essays. MIT Press, Cambridge, MA, pp209–228

Hull DL (1978) A matter of individuality. Philosophy of Science 45:335–360

Keller RA, Boyd RN, Wheeler QD (2003) The illogical basis of phylogenetic nomenclature. The Botanical Review 69:93–110

Kluge AG (2003) On the deduction of species relationships: a précis. Cladistics 19:233–239

LaPorte J (2004) Natural kinds and conceptual change. Cambridge University Press, Cambridge

Laubichler, M (2000) Homology in development and the development of the homology concept. American Zoologist 40:777–788

Love AC, Raff RA (2006) Larval ectoderm, organizational homology, and the origins of evolutionary novelty. Journal of Experimental Zoology (Molecular and Developmental Evolution) 306B:18–34

Machery E (2005) Concepts are not a natural kind. Philosophy of Science 72:444– 467

Müller GB (2003) Homology: the evolution of morphological organization. In Müller GB, Newman SA (eds) Origination of organismal form: beyond the gene in developmental and evolutionary biology. MIT Press, Cambridge, MA, pp52–69

Okasha S (2002) Darwinian metaphysics: species and the question of essentialism. Synthese 131:191–213

Rieppel O (2005a) Modules, kinds, and homology. Journal of Experimental Zoology (Molecular and Developmental Evolution) 304B:18–27

Rieppel O (2005b) Monophyly, paraphyly, and natural kinds. Biology and Philosophy 20:465–487

Rieppel O (2006) The PhyloCode: a critical discussion of its theoretical foundation. Cladistics 22:186–197

Rieppel O (2007) Species: kinds of individuals or individuals of a kind. Cladistics 23:373–384

Rieppel O, Kearney M (2007) The poverty of taxonomic characters. Biology and Philosophy 22:95–113

Schlosser G, Wagner GP (eds) (2004) Modularity in development and evolution. University of Chicago Press, Chicago von Dassow G, Munro E (1999) Modularity in animal development and evolution: elements for a conceptual framework for evodevo. Journal of Experimental Zoology (Molecular and Developmental Evolution) 285:307–325

Wagner GP (1989) The biological homology concept. Annual Review of Ecology and Systematics 20:51–69

Wagner GP (1996) Homologues, natural kinds and the evolution of modularity. American Zoologist 36:36–43

Wagner GP (2001) Characters, units and natural kinds: an introduction. In Wagner GP (ed) The character concept in evolutionary biology. Academic Press, San Diego, pp1–10

Wagner GP (2007) The developmental genetics of homology. Nature Review Genetics 8:473–479

Wagner GP, Misof BY (1993) How can a character be developmentally constrained despite variation in developmental pathways? Journal of Evolutionary Biology 6:449–455

Wilson RA (1999) Realism, essence, and kind: resuscitating species essentialism? In Wilson RA (ed) Species: new interdisciplinary essays. MIT Press, Cambridge, MA, pp187–207

Wilson RA (2005) Genes and the agents of life: the individual in the fragile sciences: biology. Cambridge University Press, Cambridge

Wilson RA, Barker MJ, Brigandt I (in press) When traditional essentialism fails: biological natural kinds. Philosophical Topics

Winther R (2001) Varieties of modules: kinds, levels, origins and behaviors. Journal of Experimental Zoology (Molecular and Developmental Evolution) 291:116-129