

The poverty of taxonomic characters

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Abstract. The theory and practice of contemporary comparative biology and phylogeny reconstruction (systematics) emphasizes algorithmic aspects but neglects a concern for the evidence. The character data used in systematics to formulate hypotheses of relationships in many ways constitute a black box, subject to uncritical assessment and social influence. Concerned that such a state of affairs leaves systematics and the phylogenetic theories it generates severely underdetermined, we investigate the nature of the criteria of homology and their application to character conceptualization in the context of transformationist and generative paradigms. Noting the potential for indeterminacy in character conceptualization, we conclude that character congruence (the coherence of character statements) relative to a hierarchy is a necessary, but not a sufficient, condition for phylogeny reconstruction. Specifically, it is insufficient due to the lack of causal grounding of character hypotheses. Conceptualizing characters as homeostatic property cluster natural kinds is in accordance with the empirical practice of systematists. It also accounts for the lack of sharpness in character conceptualization, yet requires character identification and re-identification to be tied to causal processes.

Introduction

Only 18 years old, Willi Hennig (1931 [(1978, p. 193)]) perceived the need to defend systematics against attacks from biologists who ridiculed systematists as “dried skins’ zoologists” and “species makers.” Years later, Hennig (1950, 1966) laid the groundwork for the ‘cladistic revolution’ in taxonomy (Hull 1988), which some compare to the Darwinian revolution in its significance (Kühne 1978; Dupuis 1990). Today, biosystematics has regained a reputation of an indispensable scientific discipline, in part due to the current biodiversity crisis. Sterelny and Griffiths (1999, p. 379) paraphrased a famous statement from Theodosius Dobzhansky (1973) as “nothing in biology makes sense except in the light of its place in phylogeny”, and concluded that systematics plays a “critical, foundational role” in all fields of evolutionary biology.

However, at least one philosopher has raised concerns regarding the currently fashionable ‘theory-free’ approach to character analysis in systematics. According to Richards (2002, 2003), there exists no one, agreed upon way of individuating characters, such that what constitutes a character largely boils

down to what can successfully be communicated to other systematists as a (useful) character. Recognizing, at least implicitly, the difficult problem of character conceptualization, Griffiths (1999, p. 225) suggested that “cladistic analysis can proceed from a list of arbitrary measurements by looking for congruence among the evolutionary trees produced by different measurements.” Such an argument relies on the “synergistic power of evidence” (Lipton 2004, p. 204), where evidence is acknowledged never to be certain, but confidence in the inferred phylogeny increases with an increasing number of congruent trees generated by separate sets of data.

Griffiths’ (1999) argument may relate more easily to molecular than to morphological data. Morphological homologues are complex structures that are subject to change through time if ontogeny is considered, and even more complex if composition (e.g., cell type) is a factor in initial similarity assessment (Patterson 1988). Furthermore, morphological homologues are ‘anatomical singulars’ (Riedl 1978, p. 52), subject to the ‘test of conjunction’ (Patterson 1982): the homology of human arms and bird wings as tetrapod forelimbs would be refuted by the existence of angels with both arms and wings (Patterson 1988). Molecular data by comparison are without ontogeny, they cannot be subjected to the test of conjunction, and controversy exists whether homology should be assessed at the nucleotide level or the sequence level (Wheeler, 2001a, b). Especially in the case of non-coding regions, congruence does play a much more decisive role in homology assessment for molecular data. In addition, the alignment of multiple sequences of different lengths faces the problem of whether and/or how to insert gaps to obtain the ‘best’ alignment. This is accomplished by user-specified ‘gap costs’, which entail a degree of subjectivity.

To circumvent these issues, an optimization alignment procedure has been proposed which maximizes parsimony of alignment relative to each possible tree for the terminal taxa under analysis (Wheeler 2001a, b). In this procedure, each tree topology itself ‘feeds back’ into the alignment to make it maximally parsimonious relative to a particular topology. As a consequence, homology relations between sequences may shift relative to different tree topologies, such that alignment becomes a dynamic process that is influenced by hypotheses of possible relationships and the parsimony optimality criterion. Homology relations consequently shift with changing tree topologies, which is a difference from multiple sequence alignment prior to analysis. In the latter case, the putative homology relations established by alignment remain stable, i.e., fixed, relative to changing tree topologies, as is also the case for morphological characters.

Given problems of alignment, a largely algorithmic approach (in terms of congruence) is being pursued in the analysis of increasingly larger data sets in molecular systematics. An increasingly algorithmic approach to characters has become predominant in the analysis of morphological characters as well, under the paradigm of a total evidence approach that combines all available character data without critical evaluation of homology hypotheses. Indeed, the

congruence of characters (coherence of character statements: Rieppel 2004) relative to a hierarchy has become accepted as the sole arbiter of homology vs. non-homology (homoplasy) by many contemporary systematists, irrespective of the nature of the data (Rieppel 2005a). In an effort to avoid theory-ladenness of character statements, systematics has moved towards an operationalist approach to character delineation (Kearney, in press), where theoretical input into the process of character conceptualization is rejected in favor of an appeal to mere congruence in the evaluation of whatever character hypothesis is being proposed (e.g. Kluge 2003, 2004; O'Leary et al. 2003).

It is the purpose of the present paper to analyze the different ways in which systematists identify and re-identify morphological characters in order to demonstrate that this cannot be achieved in a theory-free way. Instead, theoretical input is required at all levels of character conceptualization in morphology-based systematics. We propose to conceptualize characters relevant for phylogeny reconstruction as homeostatic property cluster natural kinds (Boyd 1991, 1999). This not only matches the actual empirical research practice of systematists, but also mandates the consideration of causal relations (e.g., of inheritance, development, and function) in character conceptualization. If phylogenetically relevant characters are viewed as HPC natural kinds, then the associated natural kind terms must have explanatory power, i.e., some causal grounding in theories of ontogeny, phylogeny, and evolution. Characters recognized as homologues (such as the vertebral column discussed below) can share a common 'stereotype' and common causal grounding, and yet be built in different ways in different taxa, as is indeed the case. Homeostatic property cluster natural kinds allow for some degree of indeterminacy, as is often encountered by systematists in character conceptualization, and yet constrain this indeterminacy by requiring taxonomic characters to enter causal relations. From this perspective, it is the problem of character conceptualization that takes conceptual priority over tree reconstruction (Wagner 1994), and not the other way around (Härilin 1999). Finally, the conceptualization of morphological homologues as tokens of homeostatic property cluster natural kinds allows these to be historically delimited (Griffiths 1999; Wilson 1999; Keller et al. 2003), as is required for evolutionary entities.

Ostensive indication of systematic characters

Richards (2002) identified an important component in the individuation of characters by systematists, which is the ostensive indication of paradigm exemplars. Indeed, for Kluge (2003, p. 366), it is "ostensive definition ... not similarity, that count[s]" in character individuation. However, ostension alone generally remains radically underdetermined (Quine 1964): if a native speaker uttered 'gavagai!' while pointing at a rabbit's heart, the English speaking listener could not know whether she meant 'detached rabbit part', 'vertebrate heart', 'four chambered heart', or 'let's have this for lunch!' Pointing at

putatively equivalent constituent parts of two or several organisms in an effort to establish some sameness-relation (as is the relation of homology) will therefore have to be followed up with, or accompanied by, a description. This description, in turn, establishes a stereotype for the kind of parts in question, but not necessarily also the correct extension of the corresponding kind term (Putnam 1996). Mere ostensive indication remains too underdetermined to mark out a theoretically relevant natural kind, i.e., a kind with explanatory value. Ostension in character conceptualization that involves paradigmatic exemplars establishes only a *structural kind* (Mahner and Bunge 1997, p. 268). Later investigation may show that such a structural kind corresponds to a historically delimited natural kind, the tokens of which are homologues (Rieppel 2005b).

The empirical work of systematists typically involves establishing the stereotype of a structural kind as a first step towards character conceptualization that is hoped to at least approximately (and defeasibly) capture a causally efficacious property (Sober, 1981; Shoemaker 2003). As a systematist sets out to reconstruct the phylogenetic relationships of a certain set of organisms that serve as exemplars for the taxa that they represent, she proceeds to compare the selected specimens in terms of properties that are instantiated by their parts. What is of interest in this comparison are not simply intrinsic properties of the organisms under consideration, but relational properties that would establish a ‘sameness’-relation between constituent parts of the organisms. In systematics, such a ‘sameness’-relation is called homology, where ‘sameness’ is due to (is causally explained by) common ancestry. Homology is the relation between homologues, homologues are ‘namesakes’ (Williams 2004), i.e., constituent parts of organisms to which the same term, i.e., a general name or natural kind term, refers or applies. The relation of homology itself is not empirically accessible, but must be inferred from a comparison of the organisms under analysis and their parts. The foundation of phylogeny reconstruction, therefore, is an initial comparison of the organisms under analysis in terms of a three-place-relation: two things may be of a more similar kind than a third thing (Janich, 1993; Mahner and Bunge 1997). However, as Sober (1984, p. 336; see also Ruse 1988, p. 60; Dupré 1993, p. 45; Hull 1999; Sterelny and Griffiths, 1999, p. 196) noted: “As philosophers have long recognized, similarity without theory is empty”. This means that even at that initial stage of comparison, statements of similarity are character statements with propositional content (Rieppel, 2004).

To initially establish such potentially theoretically relevant similarity relations, systematists must use theoretically relevant ‘pointers’, such as relative topological relations and connectivity of parts (morphological, molecular). The use of these ‘pointers’ rests on the presupposition that topology and connectivity are proximally rooted in the generative mechanisms of development which, in turn, are ultimately rooted in the phylogeny of those organisms (Rieppel and Kearney 2001; Rieppel 2005b). But presuppositions may turn out to be wrong. Sometimes these guidelines are not applicable (e.g., red vs. blue

tails of birds compared to birds without a tail); in other cases they may be misleading (due to convergence or reversal). Or these guidelines may themselves be subject to evolutionary change (through ontogenetic repatterning: see the discussion below). But this is only to concede that systematists sometimes make mistakes, that what is initially proposed as a potentially theoretically relevant similarity relation may, upon further investigation, turn out to be useless for scientific theory construction, i.e., for phylogeny reconstruction.

Rieppel and Kearney (2002) argued that the initial similarity relation useful in phylogeny reconstruction should not be established *simpliciter*, in the sense of the primitive, innate, unanalyzed, or unanalyzable ‘similarity’ of Goodman (1965, 1972), Quine (1994), and Hull (1999). Owen did not define homology in terms of similarity, but rather in terms of ‘sameness’, i.e., the ‘same’ organ in different animals under every variety of form and function (Panchen 1994; Williams 2004). If this is the correct homology concept, then there can be no theory-free approach to character conceptualization. The theoretically relevant similarity relation that delivers the promissory notes for potential homology is based on the relative topological position and connectivity of constituent parts of an organism (both morphological and molecular) in their temporal (ontogenetic) and spatial (ontogenetic, molecular) manifestations. If there is any perceptual ‘sameness’ to be had in the initial act of ostension, it has to be of this topological kind. There is no perceptual ‘sameness’ in the shape, form or function of the lower jaw of a shark and that of the outermost ear-ossicle of a mouse, but there is perceptual topological correspondence (during early ontogenetic stages). Rieppel (2003) compared these classic operational criteria of homology (Remane 1952) to ‘correspondence rules’ which, once stripped of their connotations with sense datum theory and verificationist criteria of meaning, imply nothing more than either an experimental setup or an observational procedure (Nagel 1961).

Correspondence rules are conventional, but they need not be arbitrary. Indeed, the operational criteria of homology have empirically been found to be eminently successful in the reconstruction of the tree of life (Remane 1952; Wickler 1967; Riedl 1978), supporting the presupposition that they are at least to some degree rooted in theories of development and evolution. In Boyd’s (1991, 1999) terms, their use seems to be well aligned with the causal structure of the world, at least to some degree, and defeasibly so (Rieppel and Kearney 2002). The use of criteria of homology, such as topology and connectivity is not, therefore, theory free. Those criteria do not deliver ‘operational definitions’ such as ‘an acid is whatever turns blue litmus paper red.’ Instead, topology and connectivity play an important role in development, and the evolutionary transformation of morphology (and behavior: Wickler 1967) is expressed through the preservation and/or transformation of developmental trajectories. It is precisely the problems that result from the evolutionary transformation of developmental trajectories (ontogenetic repatterning: see below) that show that the criteria of homology do not yield straightforward operational definitions. A similar use of theoretically informed correspondence

rules is known in molecular systematics: “Alignment of sequences requires explicit and objective rules if inferences of positional homology are to be robust” (Hillis 1994, p. 349; but see Wheeler 2001a, b). Rieppel and Kearney (2002) discussed several empirical examples of the application of those correspondence rules and the problems that occur when such criteria are abandoned.

Similarity relations that are based on topology and connectivity are epistemically accessible to systematists (for an early illustration see Belon 1555), but they do not necessarily satisfy Sober’s (1981) principle of causal efficacy. A second step that involves scientific theory construction is required. The fact that the ‘structural kinds’ of comparative morphology may be recognized as theoretically relevant natural kinds was pointed out by Hennig (1950, p. 26), and is also inherent in Darwin’s re-conceptualization of homology (Kitcher, 1993, p. 32). Darwin (1859) essentially took Owen’s non-evolutionary, structural concept of homology, and added the time dimension (Wagner 1994): homology was explained differently, but the referents of homology statements remained the same. Whether used by Owen or Darwin, the referent of the term ‘vertebral column’ was the same, but unlike Owen, Darwin explained the fact that all vertebrates share a vertebral column via common ancestry. “On my theory, unity of type is *explained* by unity of descent” (Darwin 1859, p. 206).

Homologues as natural kinds

Rieppel and Kearney (2002) argued that the reason that the traditional operational criteria of homology have worked so well is because they are approximately, and defeasibly, aligned with the causal structure of embryonic development that is necessarily causally linked to morphological evolution. Embryonic development is hierarchically structured, as is the relation of homology, and phylogeny. Embryonic development has furthermore been recognized as modular (Raff 1996; West-Eberhard 2003), on which basis Winther (2001, p. 117) concluded, “structural and developmental modules are the traditional units for claims about homology.” Developmental modules have in turn been claimed to be natural kinds (Wagner 1996, 2001; Brandon 1999; Rieppel 2005b), so that homologues might be conceptualized as natural kinds, too. In order to avoid a notion of ‘natural kind’ that is too strong for biology, Wagner (2001) invoked Boyd’s (1991, 1999) ‘homeostatic property cluster natural kind’ as the appropriate concept for developmental modules; the same concept can be applied to homologues.

One of the classic, deeply ‘entrenched’ (Wimsatt 1986; Schank and Wimsatt 2000) homologies of vertebrates is the vertebral column. People tend to use the term ‘vertebral column’ in a loose fashion, meaning some sort of backbone that supports the vertebrate body. In fact, there exist all sorts of vertebral columns. In sharks, vertebral centra are formed by calcified cartilage that invades the notochord. In sturgeons, four bony plates (basidorsals,

basiventrals, interdorsals and interventrals) per body segment are applied to either side of the notochord. Trout have a single fully ossified centrum per body segment that almost completely replaces the notochord. This is a general pattern for teleost fishes, but the sister-taxon of teleosts, the bowfin (*Amia*), can have two centra per body segment over a variable stretch in the posterior part of its vertebral column (a phenomenon known as ‘diplocoely’). In fossil amphibians (labyrinthodonts), there is a set of bony elements (pleurocentra, hypocentrum, neural arch), which surround, and partially or fully replace, the notochord, combining with each other in a variable pattern. Other fossil amphibians, as well as all extant ones, have a single ossification forming one centrum per body segment. But whereas the vertebral centrum in frogs and salamanders is homologous to the labyrinthodont hypocentrum, that of amniotes is thought to have evolved from the pleurocentra. Evidently, if there is a natural kind ‘vertebral column’, it can only be a homeostatic property cluster natural kind (Boyd 1991, 1999): cartilage and bones surrounding or invading the notochord in variable patterns. Yet the vertebral column is still homologous throughout vertebrates – it shares the appropriate stereotype calibrated on topology and connectivity (dorsal position in the body, connected to the skull anteriorly, surrounding the spinal cord, underlain by the aorta dorsalis, etc.) that serve as criteria of identification and re-identification. The criteria of topology and connectivity are furthermore well aligned with the causal processes of ontogeny. At the level of Vertebrata, the causal grounding of the natural kind term ‘vertebral column’ lies in the genomic instruction for sclerotome cells to migrate medially from the resegmented somites towards the notochord, and to then differentiate into chondroblasts and osteoblasts that will then form cartilagenous and eventually bony elements within and around the notochord, and around the spinal cord, in a variable pattern. It is impossible to give a single (definite) description of ‘the vertebral column’ across vertebrates, but it is possible to identify somite re-segmentation, sclerotome formation, cell migration and differentiation as the causal processes that result in the formation of vertebral columns. All of these causal processes are constrained by topology and connectivity. It is these underlying causal relations of development that determine the extension of the natural kind term ‘vertebral column’, and that establish the homology of the vertebral column across vertebrates, not as a superficial similarity relation, but as a ‘sameness’ relation that suggests a common evolutionary origin. The suggestion of a common evolutionary origin of the vertebral column requires further support through phylogenetic analysis (congruence), however, not only because topology and connectivity are defeasible criteria of homology, but also because developmental trajectories are themselves subject to evolutionary change.

The property of having four limbs is a similarly deeply entrenched homology of tetrapods, but snakes have (at best) only hind limbs (Rieppel et al. 2003) or rudiments thereof (Kley et al. 2002); most have no limbs at all. But if the presence of four limbs is a homology of tetrapods, and if homologues are homeostatic property cluster natural kinds, then snakes do not have ‘no limbs’,

but ‘modified limbs’ instead (Platnick 1978), their loss being an extreme case of modification that affects most, but not all, snakes. Indeed, the presence of (hind) limbs in some snakes, and their loss in others, is rooted in the same causal mechanisms that govern the development of limbs in other squamate reptiles (Cohn and Tickle 1999; Sanger and Gibson-Brown 2004). This example is particularly useful in showing that character conceptualization is not based on semantic analysis (most people use the term ‘snake’ to refer to all sorts of limbless reptiles that include both non-ophidian squamates as well as snakes), nor does it result in the intensional (analytic) definition of taxa (on which basis snakes could not be tetrapods: Rowe 1987). Character conceptualization is a matter of empirical research and defeasible scientific theory construction.

The transformational vs. the generative approach to character conceptualization

There are two major paradigms under which characters are delineated in contemporary, morphology-based systematics. One is the transformational approach, where characters gleaned from adult phenotypes are conceptualized as stages of a transformation series (Hennig 1966; Wiley 1981; Grant and Kluge 2004). The other paradigm is the generative approach, where characters are thought to be individuated through ontogenetic development (Rieppel 1993a; Oyama et al. 2001). The turtle shell (carapace) provides a prime example to illustrate the transformational vs. the generative approaches to character conceptualization and their consequences (for more details see Burke 1989; Rieppel and Reisz 1999; Rieppel 2001; Gilbert et al. 2001).

The turtle body is encased in a dorsal carapace and a ventral plastron. Armadillos, crocodiles, and most bony fishes (certainly the ‘primitive’ ones) also have a body covered by bony plates, which remain small, and may be sutured to one another or separated by gaps. Such bony plates covering the body of many vertebrates are called scales in fishes, osteoderms in tetrapods. The latter term refers to the fact that these elements are formed by direct ossification in the deep layer of the skin (dermis). As such, osteoderms are exoskeletal elements. Endoskeletal elements are those that develop deeper in the body, and that typically (at least primitively) undergo cartilagenous preformation prior to ossification. The vertebral column, ribs, and limb bones are examples of endoskeletal elements (for a definition of exoskeleton versus endoskeleton see Patterson (1977)).

A transformational approach to character conceptualization explains the evolution of the turtle shell through a gradual increase in numbers and eventual fusion of osteoderms, which are also present in “pareiasaurs, presumed turtle relatives” (Romer 1956, p. 437). This approach is based on the comparison of adult phenotypes, and seeks to bridge the ‘morphological gap’ (Lee 1993) between adult structures by the search for (sometimes hypothetical) intermediate stages. The supporting phylogenetic theory is that turtles are nested within a clade of Paleozoic reptiles (pareiasaurs), of which the more

derived members show an increasingly elaborate development of osteoderms (Lee 1993). The only thing necessary to derive the turtle carapace from the osteoderm covering of a derived pareiasaur such as *Anthodon* is the fusion of relatively small osteoderms into larger and regularly arranged bony plates. There is a snag, however, in that the shoulder blade (scapula) lies outside the ribcage in all tetrapods except for turtles. Under the transformational paradigm, this issue is resolved by the assumption of a gradual backward shift of the pectoral girdle to a level inside the rib cage in turtles.

However, no backward shift of the pectoral girdle is detected through direct observation of the ontogeny of turtles (Burke 1991). Instead, it is the ribs that grow out to a position superficial to the scapula (Burke 1989). The topological relations of the ribs undergo observable ontogenetic change, but the ribs still retain their typical developmental connectivity. The turtle carapace is first mapped out in the embryo as a carapacial disk composed of the thickened deep layer of the skin (dermis). An inductive signal, emanating from the margins of this carapacial disk (Burke 1989) and triggered by the expression of co-opted genes in a novel system (Kuraku et al. 2005; Gilbert et al. 2004), re-directs the migration of those sclerotome cells that will form the ribs to a more superficial position outside the scapula. The cartilagenous ribs thus come to develop within the dermis layer of the carapacial disk. Perichondral ossification of the ribs and their lateral expansion within the carapacial disk by the formation of trabecular bone eventually forms the costal plates of the carapace (ossification of the endoskeletal neural arches of the vertebrae similarly contributes to the formation of the neural plates in the carapace). The turtle carapace thus re-combines endoskeletal and exoskeletal elements in a unique, complex, and entirely novel way. The turtle shell is a highly integrated, novel system, homologous throughout turtles and tied into a network of genetic and developmental causes (Kuraku et al. 2005; Gilbert et al. 2004). Authors who defend the transformational paradigm suggest that such “developmental specialization does not provide any hint as to the way in which this pattern evolved phylogenetically” (Carroll 1988, p. 210). Under the generative paradigm such radical recombination of developmental resources in novel ways (West-Eberhard 2003) during phylogeny may indicate some incompleteness of the transformational paradigm (Gould 1977; Rieppel 2001). Turtles may, indeed, not be related to pareiasaurs after all (Rieppel and Reisz 1999; Iwabe et al. 2005, and references therein).

This example documents not only the power that the concept of transformation series holds over the thought processes of evolutionary biologists and systematists, it also documents the potential shortcomings of conceptualizing characters as states of transformation of adult phenotypic traits. The turtle shell is not a singular example: no transformation series has to date been formulated for the modification of a pentadactyl reptile limb to an ichthyosaur flipper, and no transformation series has been proposed for the transformation of the limbs of a rock-dwelling agamid lizard to those of a tree-dwelling chameleon. This is not to say that stepwise transformation of adult ancestral

phenotypic structures does not occur. Of course it does, but it is not the only mode of morphological evolution, and hence it cannot be the only mode of character conceptualization.

‘Splitters’ and ‘lumpers’

The notion of ‘splitters’ and ‘lumpers’ was first introduced by Simpson (1961, p. 138) to refer to different dispositions amongst alpha taxonomists in their treatment of species or higher taxa. Richards (2002, 2003) expanded this notion to different dispositions amongst systematists in their treatment of characters, and noted the important consequences of this threat of subjectivism in character conceptualization for phylogenetic analysis. In other words, there exists a sliding scale between more coarse-grained or more fine-grained character conceptualization.

Oversplitting can occur in at least two ways (see also Ruse 1988, p. 60): the oversplitting of a developmentally, or functionally, correlated character complex (Richards 2003, used the mammalian middle ear ossicles as an example), or the separate (i.e., redundant) coding of serially homologous characters (Richards 2002, used the spines of porcupines as an example). Both can result in an overweighting of characters for phylogenetic analysis. Conversely, the phylogenetic signal may be distorted by a lumping of characters on grounds of mistaken (or at least untested) presuppositions of developmental, or functional, correlation or constraints.

Chameleon hand and feet provide a good illustration of the problem. Unlike any other ‘lizards’ (non-ophidian squamates), chameleons evolved opposing digits that allow them to grasp branches, a condition termed zygodactyly. According to Raff (1996, p. 353), “vertebrate forelimbs and hind limbs are clearly serial homologues.” This could mean that zygodactyly in the fore- and hind limbs of chameleons should be conceptualized as a single character with a special developmental background and functional role that suggest a unique evolutionary origin. However, in the hand, two outer digits (IV and V) oppose three inner digits (I, II and III), whereas in the foot, three outer digits (III, IV, V) oppose two inner digits (I, II). Does that make for two characters to capture the evolution of zygodactyly? In the literature, zygodactyly in chameleons has been conceptualized in terms of nine, putatively independent character-states of hands and feet (Estes et al. 1988; additional characters are coded for potentially correlated changes in other parts of the chameleon appendicular skeleton).

In the case of chameleons, splitting, or oversplitting, of zygodactyly into numerous character-states, is arguably unproblematic for the reconstruction of phylogeny. This is because, among ‘lizards’, *all* and *only* chameleons exhibit zygodactyly, such that this unique condition (called autapomorphic by systematists) is not informative for the analysis of the relationships of chameleons with other groups of ‘lizards.’ However, the number of characters coded for

zygodactyly will be relevant in studies of evolutionary transformation rates that involve chameleons.

In other contexts, oversplitting of structures can be more problematic for the results of phylogenetic analysis. For example, an intense debate has recently surrounded the discovery of fossil, mid-Cretaceous snakes with well-developed hind limbs from marine deposits of the Middle East (Caldwell and Lee 1997; Zaher and Rieppel 2000; Rieppel and Kearney 2001). The debate relates to the fact that these fossils exhibit a skull anatomy that resembles that of advanced (macrostomatan) modern snakes such as boas and pythons, whereas the presence of well-developed hind limbs would suggest that they are the most primitive snakes known, sister-group to all extant snakes. Boas and pythons, as well as all more basal (more 'primitive') snakes (such as blind snakes, thread snakes, pipe snakes and shield tails) retain much-reduced pelvic and hind limb rudiments (Kley et al. 2002). Placing the fossil snakes with well-developed hind limbs as advanced macrostomatans (i.e., with boas and pythons) raises the possibility that limbs were re-developed from rudiments in these fossil snakes (Greene and Cundall 2000; Tchernov et al. 2000), something that many find biologically implausible (e.g., Coates and Ruta 2000; Rage and Escuillié 2003). Alternatively, this phylogenetic hypothesis might imply that limbs were lost more than once and/or that 'missing' fossil snake lineages might resolve this case of character conflict (see discussion in Rieppel et al. 2003).

The empirical question that arises in this context is how many characters to code for the skull as opposed to the limb? Splitting the limb into a large number of separately coded characters will result in a grouping of all extant snakes on the basis of a corresponding number of 'limb loss characters.' Notwithstanding their advanced skull structure, the fossils would thus be placed as the most basal snakes, sister-taxa to all extant snakes (and potentially documenting a marine, as opposed to a terrestrial, origin of snakes). If, on the other hand, the presence of well-developed hind limbs is coded as a single character, or balanced by an equivalent degree of (over-)splitting of skull characters, then the skull characters may override the signal from the limb characters, resulting in a placement of the fossil snakes with advanced macrostomatans. Given the total evidence at hand at the time, Tchernov et al. (2000, p. 2012) noted in their analysis of the phylogenetic relationships of one of these snake taxa (*Haasiophis*) that 15 limb characters were sufficient (and required) to pull the fossil snakes with well-developed hind limbs to a basal position outside all extant snakes. But, as noted by Richards (2002, 2003), it is a decision to be taken by the investigator how many limb characters or skull characters to code. Further, either phylogenetic result can be favored if characters are not required to have any causal grounding, but are simply based on the investigator's disposition (Kearney, in press).

Oversplitting of characters potentially violates the theoretical assumption that each of those characters evolved independently. Vane-Wright (2001, p. 592) deplored the lack of a sharp "stopping rule" for practical character subdivision, and indeed, there cannot be such a rule. A putatively a-theoretical

approach to character conceptualization (Härlin 1999) may easily identify ways to break up the hind limbs of fossil snakes (with 12 individual elements at least partially preserved in the best fossil, *Haasiophis*: Tchernov et al. 2000) into 15 or more characters, but the biological plausibility of such a strategy will remain questionable. To conceptualize homologues as homeostatic property cluster natural kinds may not allow drawing a sharp line for how many characters can or should be coded for a structural complex, but it does require theories of inheritance, of development, and of functional anatomy to bear on the problem of character conceptualization, because tokens of natural kinds are supposed to take part in causal processes. This stands in contrast to the a-theoretical approach to character conceptualization, which often results in the kinds of irresolvable phylogenetic debates described above due to differing dispositions of systematists in character coding (Rieppel and Kearney 2001, 2002).

Indeterminacy

Kitcher (1993, p. 103) registered surprise as to how much ambiguity scientists are prepared to entertain in their theory construction. “Scientists usually have the intention of referring to natural kinds, picking out the real similarities in nature” (Kitcher 1993, p. 104), but if uncertain, systematists may deploy ambiguous terms or descriptions. LaPorte (2004) identified vagueness – open texture – for many natural kind terms, whose meanings may get refined or even change by ongoing empirical investigation. It is no surprise that ambiguity abounds in character conceptualization, especially if the latter proceeds uncritically. But there also appear to be cases where ambiguity seems unavoidable, as in cases of ontogenetic repatterning. Ambiguity of a different kind also obtains in cases of very simple transformation series, such as a step from the presence to the absence (i.e., loss) of a structural element.

The zygodactylous chameleon foot is an example of ontogenetic repatterning (Rieppel 1993b). In all ‘lizards’ (non-ophidian squamates) with well-developed limbs, a single large cartilaginous block forms in the proximal tarsus during ontogeny. Later, two ossification centers appear in that proximal tarsal cartilage, first the astragalus, then the calcaneum. Chameleons also form a proximal tarsal cartilage, but only a single ossification center ever appears within it. Should it be called the astragalus, because this is the first element to appear in the proximal tarsus in other ‘lizards?’ But since it is known that the relative timing of developmental events can change (e.g., Gould 1977), it might also be the calcaneum. There is no evidence that allows discrimination between the two choices. Due to this ambiguity, the element has been called the astragalo-calcaneum (Estes et al. 1988), but then this seems to imply fusion of these elements, when no fusion of two ossifications is ever observed during chameleon ontogeny. Although ambiguous, the situation is not problematic in this particular case, because zygodactyly is uninformative (autapomorphic) with respect to chameleon relationships to other squamates.

However, other problematic examples of ‘simple transformation series’ involve potentially informative characters. The plesiomorphic squamate condition (the ‘primitive’ condition for the clade that comprises ‘lizards’, amphisbaenians, and snakes) is to have two bones behind the orbit. Of those, the anterior one is called the postfrontal, the posterior one the postorbital. This condition is observed amongst iguanas for example. Most lizards retain only a single bone behind the orbit: is it the postfrontal, postorbital, or a fused postorbito-frontal? If developmental data are available, and if two separate elements can be observed to fuse during ontogeny, the element may be called a postorbito-frontal. If no ontogenetic data are available, or if such data are available but document the presence of only a single bone throughout development (as is the case in all those snakes that do retain a bone behind the orbit), the application of either the term ‘postfrontal’ or the term ‘postorbital’ to the single element must remain ambiguous. There is no way of knowing which one of the two bones was lost. Pythons add more to the problem by having two bones related to the orbit, of which the anterior one is located above, rather than behind, the orbit. Do pythons have an anteriorly displaced postfrontal together with a postorbital, or did a new element, a ‘supraorbital’, evolve in this clade? Only entrenchment through continued use (Goodman, 1965), not insight into underlying causality, has fixed the bone above the orbit in pythons as the referent of the term ‘supraorbital’ amongst herpetologists.

Problems of establishing the correct nature of the ossifications behind the orbit have led herpetologists to take recourse to terms with partial reference (Field 1973; for a brief account of the concept of ‘partial reference’ see Devitt 1997; Lycan 2000; ‘reference potential’ in Kitcher 1993). Abandoning a stipulative approach to the definition of circumorbital elements (Estes et al. 1988), Scanlon and Lee (2000, supplementary material) proposed the following revised character conceptualization: “*posterior orbital ossifications*: present/absent; one/two”. A later version that further illustrates this unavoidable ambiguity of reference reads: “*Postorbitofrontal ossification(s)* in adults. 0, one discrete ossification, conventionally termed postorbitofrontal ... 1, two discrete ossifications, conventionally termed the postfrontal and postorbital. 2, no discrete ossifications... “ (Lee and Scanlon 2002, p. 356).

This, again, is not a singular example. In typical ‘lizards’ (non-ophidian squamates), the lower jaw is suspended via the quadrate bone from two bones in the skull roof: the medial supratemporal and the lateral squamosal. Only one of these bones is retained in the skull roof of gekkotans (geckos and pygopods), identified as the ‘squamosal’ (Underwood 1957). In snakes, a single bone again is preserved, this time called the ‘supratemporal’ (Estes et al. 1988). The application of ‘supratemporal’ to snakes is a matter of pure entrenchment (sensu Goodman 1965) due to prior and continuing use of this term in that way by an overwhelming majority of herpetologists. Such entrenchment can have theoretical consequences. A relationship of snakes with gekkotans has indeed been proposed (Iordanski 1978), such that applying the same or different names to the bone serving the jaw suspension (remember that homologues are

'namesakes': Williams 2004) could potentially have theoretical consequences (a snake – gekkotan sister-group relationship is not currently under consideration, however).

The question naturally arises whether such unavoidably ambiguous character conceptualizations are good enough to be used in phylogenetic analysis? Some would not admit such characters into the analysis, others might conclude that they should be retained as long as "better than chance predictions" (Griffiths 1999, p. 216) about their instantiations can be made. But whatever the nature of the characters so conceptualized, they cannot be natural kinds, they are at best structural kinds.

Discussion and conclusions

The identification and re-identification of morphological characters in systematics requires theoretical input at various levels. Empirical research and theory construction in systematics typically proceeds from the establishment of a structurally grounded 'sameness'-relation based on topology and connectivity of constituent parts of organisms to the causally grounded 'sameness'-relation of homology. The first step yields structural kinds that have the potential to be natural kinds, the second (homeostatic property cluster) natural kinds. The recognition of structural kinds as natural kinds is mediated by research into the causal grounding of character statements (in theories of inheritance, development, and functional anatomy), and is further supported by the congruence (i.e., coherence) of character statements relative to a hierarchy in phylogeny reconstruction.

Topology, connectivity, and congruence evidently play a major role in homology assessment in molecular systematics also, both at the nucleotide as well as at the sequence level (Wheeler 2001a, b). However, problems of alignment both at the nucleotide and at the sequence level, as well as the shifting domains of homology under the direct optimization alignment procedure (Wheeler 2001a, b), render the comparison of molecular and morphological relations of homology problematical (Patterson 1987, 1988). We argued above that congruence of morphological characters is a necessary, but not a sufficient, condition for homology. Given the exceedingly complex relations that anchor nucleotides in causal networks of gene expression and regulation, molecular systematists today are focusing on a predominantly algorithmic approach. This approach seeks maximal congruence of as many data as possible under the assumption that a statistically significant degree of congruence would not obtain due to chance alone. This does not mean, however, that molecular systematists do not look towards future improvements in methodology that would provide a stronger grounding of homology relations in causal processes.

It is perhaps the methodologically motivated desire to match an ever increasing amount of molecular data with a proportionate number of morphological

characters in a ‘total evidence approach’ that has fostered the idea of the logical primacy of trees over characters, and resulted in an over-reliance on character congruence as the only arbiter of morphological homology (e.g., Härlin 1999; see Disney 2003, for a response). Character congruence with respect to a hierarchy will help sort putative homology from homoplasy, but with respect to morphological characters, it cannot solve problems of ambiguous character definitions, poorly or even wrongly conceptualized transformation series, or oversplit or overlumped character complexes. What Richards (2002, 2003) put his finger on is the trend towards an increasingly theory-free approach to characters, compensated for by an increasingly large number of characters to be used in phylogenetic analysis (Rieppel and Kearney, 2002). This research program results in what Wägele (2004, p. 109) called “phenetic cladistics: elegant analyses with many sources of error.” The problem with this approach is that an appeal to causal relations has been buried under the logic of numbers. But biology has a long tradition of doing much better: evaluating characters in a causal (developmental, functional) context. Such would indeed seem to be required if systematics is to play the foundational role in evolutionary studies that Sterelny and Griffiths (1999) request for it.

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References

- Belon P. 1555. *L’Histoire de la Nature des Oyseaux*. Guillaume Cavellat, Paris.
- Boyd R. 1991. Realism, anti-foundationalism and the enthusiasm for natural kinds. *Philos. Stud.* 61: 127–148.
- Boyd R. 1999. Homeostasis, species, and higher taxa. In: Wilson R.A. (ed.), *Species: New Interdisciplinary Essays*, MIT Press, Cambridge, MA, pp. 141–185.
- Brandon R.N. 1999. The units of selection revisited: the modules of selection. *Biol. Philos.* 14: 67–180.
- Burke A.C. 1989. Development of the turtle carapace: implications for the evolution of a novel bauplan. *J. Morphol.* 199: 363–378.
- Burke A.C. 1991. The development and evolution of the turtle body plan: inferring intrinsic aspects of the evolutionary process from experimental embryology. *Am. Zool.* 31: 616–627.
- Caldwell M.W. and Lee M.S.Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature* 386: 705–709.
- Carroll R.L. 1988. *Vertebrate Paleontology and Evolution*. W.H. Freeman & Co., New York.
- Coates M. and Ruta M. 2000. Nice snakes, shame about the legs. *Trends Ecol. Evol.* 15: 503–507.
- Cohn M.J. and Tickle C. 1999. Developmental basis of limblessness and axial patterning in snakes. *Nature* 399: 474–479.
- Darwin Ch. 1859. *The Origin of Species*. John Murray, London.

- Devitt M. 1997. *Realism and Truth*, 2nd ed. Princeton University Press, Princeton, New Jersey.
- Disney R.H.L. 2003. Is not Hennig's method of producing cladograms as defensible as those derived from parsimony algorithms? *Bonner zoologische Beiträge* 50: 305–311.
- Dobzhansky Th. 1973. Nothing in biology makes sense except in the light of evolution. *Am. Biol. Teach.* 35: 125–129.
- Dupré J. 1993. *The Disorder of Things. Metaphysical Foundations of the Disunity of Science.* Harvard University Press, Cambridge, MA.
- Dupuis C. 1990. Hennig, Emil Hans Willi. In: Holmes F.L. (ed.), *Dictionary of Scientific Biography*, Vol. 17 (Suppl 2). Charles Scribner's Sons, New York, pp. 407–410.
- Estes R., de Quieroz K. and Gauthier J. 1988. Phylogenetic relationships within Squamata. In: Estes R. and Pregill G. (eds), *Phylogenetic Relationships of the Lizard Families*, Stanford University Press, Stanford, pp. 119–281.
- Field H. 1973. Theory change and the indeterminacy of reference. *J. Philos.* 70: 462–481.
- Gilbert S.F., Loredo G.A., Brukman A. and Burke A.C. 2001. Morphogenesis of the turtle shell: the development of a novel structure in tetrapod evolution. *Evol. Dev.* 3: 47–58.
- Gilbert S.F., Cebra-Thomas J.A. and Fraser T. 2004. Working hypothesis for the origin of the turtle shell. *J. Morphol.* 260: 294(abstr.).
- Goodman N. 1965. *Fact, Fiction, and Forecast*, 2nd ed. Bobbs-Merrill, New York.
- Goodman N. 1972. Seven strictures on similarity. In: Goodman N. (ed.), *Problems and Projects*, The Bobbs-Merrill Company, Indianapolis, IN, pp. 437–447.
- Gould S.J. 1977. *Ontogeny and Phylogeny*. The Belknap Press at Harvard University Press, Cambridge, MA.
- Grant T. and Kluge A.G. 2004. Transformation series as an ideographic character concept. *Cladistics* 20: 32–31.
- Greene H.W. and Cundall D. 2000. Limbless tetrapods and snakes with legs. *Science* 287: 1939–1941.
- Griffiths P.E. 1999. Squaring the circle: natural kinds with historical essences. In: Wilson R.A. (ed.), *Species. New Interdisciplinary Essays*, The MIT Press, Cambridge, MA, pp. 209–228.
- Härllin M. 1999. The logical priority of the tree over characters and some of its consequences for taxonomy. *Biol. J. Linn. Soc.* 68: 497–503.
- Hennig W. 1950. *Grundzüge einer Theorie der Phylogenetischen Systematik*. Deutscher Zentralverlag, Berlin.
- Hennig W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana.
- Hennig W. 1978. Die Stellung der Systematik in der Biologie. *Entomol. Germ.* 4: 193–199.
- Hillis A.L. 1994. Homology in molecular biology. In: Hall B.K. (ed.), *Homology. The Hierarchical Basis of Comparative Biology*, Academic Press, San Diego, pp. 339–368.
- Hull D.L. 1988. *Science as a Process. An Evolutionary Account of the Social and Conceptual Development of Science*. The University of Chicago Press, Chicago.
- Hull D.L. 1999. On the plurality of species: questioning the party line. In: Wilson R.A. (ed.), *Species. New Interdisciplinary Essays*, The MIT Press, Cambridge, MA, pp. 23–48.
- Jordansky N.N. 1978. On the origin of snakes. *Zool. Zh.* 57: 888–898(in Russian).
- Iwabe N., Hara Y., Kumazawa Y., Shibamoto K., Saito Y., Miyata T. and Katho K. 2005. Sister group relationship of turtles to the bird–crocodilian clade revealed nuclear DNA-coded proteins. *Mol. Biol. Evol.* 22: 810–813.
- Janich P. 1993. Der Vergleich als Methode in den Naturwissenschaften. In: Weingarten M. and Gutmann W.F. (eds), *Geschichte und Theorie des Vergleichs in den Biowissenschaften, Aufsätze und Reden Nr. 40 der Senckenbergischen Naturforschenden Gesellschaft*, Verlag Waldemar Kramer, Frankfurt a.M., pp. 13–27.
- Kearney, M. (In press). Philosophy and phylogenetics: historical and current connections. In: Hull, D. and Ruse M. (eds), *Cambridge Companion to the Philosophy of Biology*.
- Keller R.A., Boyd R.N. and Wheeler Q.D. 2003. The illogical basis of phylogenetic nomenclature. *Bot. Rev.* 69: 93–110.
- Kitcher P. 1993. *The Advancement of Science. Science without Legend, Objectivity without Illusions*. Oxford University Press, Oxford.

- Kley N., Hilton E.J. and Richmond E.J. 2002. Comparative morphology of the pelvic apparatus of snakes. *Integr. Comp. Biol.* 42: 1257(abstract).
- Kluge A.G. 2003. The repugnant and the mature in phylogenetic inference: atemporal similarity and historical identity. *Cladistics* 19: 356–368.
- Kluge A.G. 2004. On total evidence: for the record. *Cladistics* 20: 205–207.
- Kühne W. 1978. Willi Hennig 1913–1976: Die Schaffung einer Wissenschaftstheorie. *Entomol. Germ.* 4: 374–376.
- Kuraku S., Usuda R. and Kuratani S. 2005. Comprehensive survey of carapacial ridge-specific genes in turtle implies co-option of some regulatory genes in carapace evolution. *Evol. Dev.* 7: 3–17.
- LaPorte J. 2004. *Natural Kinds and Conceptual Change*. Cambridge University Press, Cambridge.
- Lee M.S.Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science* 261: 1716–1720.
- Lee M.Y.S. and Scanlon J.D. 2002. Snake phylogeny based on osteology, soft anatomy, and ecology. *Biol. Rev.* 77: 333–401.
- Lipton P. 2004. *Inference to the Best Explanation*, 2nd ed. Routledge, London.
- Lycan W.G. 2000. *Philosophy of Language. A Contemporary Introduction*. Routledge, New York.
- Mahner M. and Bunge M. 1997. *Foundations of Biophilosophy*. Springer, Berlin.
- Nagel E. 1961. *The Structure of Science. Problems in the Logic of Scientific Explanation*, Harcourt, Brace & World Inc.
- O'Leary M.A., Gatesy J. and Novacek M.J. 2003. Are the dental data really at odds with the molecular data? Morphological evidence for whale phylogeny (re)examined. *Syst. Biol.* 52: 853–564.
- Oyama S., Griffiths P.E. and Gray R.D. 2001. Introduction: what is developmental systems theory? In: Oyama S., Griffiths P.E. and Gray R.D. (eds), *Cycles of Contingency. Developmental Systems and Evolution*, The MIT Press, Cambridge, MA, pp. 1–11.
- Panchen A.L. 1994. Richard Owen and the concept of homology. In: Hall B.K. (ed.), *Homology. The Hierarchical Basis of Comparative Biology*, Academic Press, San Diego, pp. 21–62.
- Patterson C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. In: Andrews S.M., Miles R.S. and Walker A.D. (eds), *Problems in Vertebrate Evolution*, Academic Press, London, pp. 77–121.
- Patterson C. 1982. Morphological characters and homology. In: Joysey K.A. and Friday A.E. (eds), *Problems of Phylogenetic Reconstruction*, Academic Press, London, pp. 21–74.
- Patterson C. 1987. Introduction. In: Patterson C. (ed.), *Molecules and morphology in evolution: conflict or compromise*, Cambridge University Press, Cambridge, pp. 1–22.
- Patterson C. 1988. Homology in classical and molecular biology. *Mol. Biol. Evol.* 5: 603–625.
- Platnick N.I. 1978. Philosophy and the transformation of cladistics. *Syst. Zool.* 28: 537–546.
- Putnam H. 1996. The meaning of 'meaning'. In: Pessin A. and Goldberg S. (eds), *The Twin Earth Chronicles. Twenty Years of Reflection on Hilary Putnam's "The Meaning of 'Meaning'"*, M.E. Sharpe, Armonk, NY, pp. 3–52.
- Quine W.V. 1964. *Word and Object*. The MIT Press, Cambridge, MA.
- Quine W.V. 1994. Natural kinds. In: Stalker D. (ed.), *Grue. The New Riddle of Induction*, Open Court, La Salle, IL, pp. 42–56.
- Raff R.A. 1996. *The Shape of Life. Genes, Development, and the Evolution of Animal Form*. The University of Chicago Press, Chicago.
- Rage J.-C. and Escuillié F. 2003. The Cenomanian: stage of hindlimbed snakes, *Carnets de Géologie*, Article 2003/01:1–11.
- Remane A. 1952. *Die Grundlagen des Natürlichen Systems, der Vergleichenden Anatomie und der Phylogenetik*. Akademische Verlagsgesellschaft, Leipzig.
- Richards R. 2002. Kuhnian values and cladistic parsimony. *Perspect. Sci.* 10: 1–27.
- Richards R. 2003. Character individuation in phylogenetic inference. *Philos. Sci.* 70: 264–279.
- Riedl R. 1978. *Order in Living Organisms*. John Wiley & Sons, Chichester.
- Rieppel O. 1993a. The conceptual relationship of ontology and phylogeny: the taxic approach. *Evol. Biol.* 27: 1–32.

- Rieppel O. 1993b. Studies on skeleton formation in reptiles. II. The postembryonic development of the skeleton in *Chamaeleo hoehnelii* (Reptilia: Chamaeleoninae). *Herpetologica* 49: 66–78.
- Rieppel O. 2001. Turtles as hopeful monsters. *BioEssays* 23: 987–991.
- Rieppel O. 2003. Semaphoronts, cladograms, and the roots of total evidence. *Biol. J. Linn. Soc.* 80: 167–186.
- Rieppel O. 2004. The language of systematics, and the philosophy of ‘total evidence’. *Syst. Biodivers.* 2: 9–19.
- Rieppel O. 2005a. The philosophy of total evidence and its relevance for phylogenetic inference. *Papéis Avulsos Zool.* 45: 77–89.
- Rieppel O. 2005b. Modules, kinds, and homology. *J. Exp. Zool. (Mol. Dev. Evol.)* 304B: 18–27.
- Rieppel O. and Kearney M. 2001. The origin of snakes: limits of a scientific debate. *Biologist* 48: 110–114.
- Rieppel O. and Kearney M. 2002. Similarity. *Biol. J. Linn. Soc.* 75: 59–82.
- Rieppel O. and Reisz R.R. 1999. The origin and early evolution of turtles. *Annu. Rev. Ecol. Syst.* 30: 1–22.
- Rieppel O., Zaher H., Tchernov E. and Polcyn M.J. 2003. The anatomy and relationships of *Haasiophis terrasanctus*, a fossil snake with well-developed hind limbs from the mid-Cretaceous of the Middle East. *J. Paleontol.* 77: 336–358.
- Romer A.S. 1956. *Osteology of the Reptiles*. Chicago University Press, Chicago.
- Rowe T. 1987. Definition and diagnosis in the phylogenetic system. *Syst. Zool.* 36: 208–211.
- Ruse M. 1988. *Philosophy of Biology Today*. State University of New York Press, Albany, NY.
- Sanger T.J. and Gibson-Brown J.J. 2004. The developmental bases of limb reduction and body elongation in squamates. *Evolution* 58: 2103–2106.
- Scanlon J.D. and Lee M.Y.S. 2000. The Pleistocene serpent *Wonambi* and the early evolution of snakes. *Nature* 403: 416–420.
- Schank J.C. and Wimsatt W.C. 2000. Evolvability: adaptation and modularity. In: Singh R., Krimbas C., Beatty J. and Pauls D. (eds), *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*, Cambridge University Press, Cambridge, pp. 322–335.
- Shoemaker S. 2003. Causality and properties. In: Shoemaker S. (ed.), *Identity, Cause, and Mind: Expanded Edition*, Oxford University Press, Oxford, pp. 206–233.
- Simpson G.G. 1961. *Principles of Animal Taxonomy*. Columbia University Press, New York.
- Sober E. 1981. Evolutionary theory and the ontological status of properties. *Philos. Stud.* 40: 147–176.
- Sober E. 1984. Discussion: sets, species, and evolution. *Comments on Philip Kitcher’s ‘species’*. *Philos. Sci.* 51: 334–341.
- Sterelny K. and Griffiths P.E. 1999. *Sex and Death. An Introduction to Philosophy of Biology*. The University of Chicago Press, Chicago.
- Tchernov E., Rieppel O., Zaher H., Polcyn M.J. and Jacobs L.J. 2000. A new fossil snake with limbs. *Science* 287: 2010–2012.
- Underwood G. 1957. On lizards of the family Pygopodidae, a contribution to the morphology and phylogeny of the Squamata. *J. Morphol.* 100: 207–268.
- Vane-Wright R.I. 2001. Taxonomy, methods of. In: Levin S. (ed.), *Encyclopedia of Biodiversity*, Vol. 5. Academic Press, New York, pp. 589–606.
- Wägele K. 2004. Hennig’s phylogenetic systematics brought up to date. In: Williams D.M. and Forey P.L. (eds), *Milestones in Systematics*, CRC Press, Boca Raton, FL, pp. 101–125.
- Wagner G.P. 1994. Homology and the mechanisms of development. In: Hall B.K. (ed.), *Homology. The Hierarchical Basis of Comparative Biology*, Academic Press, San Diego, pp. 273–299.
- Wagner G.P. 1996). Homologues, natural kinds and the evolution of modularity. *Am. Zool.* 36: 36–43.
- Wagner G.P. 2001. Characters, units, and natural kinds. In: Wagner G.P. (ed.), *The Character Concept in Evolutionary Biology*, Academic Press, San Diego, pp. 1–10.
- West-Eberhard M.J. 2003. *Developmental Plasticity and Evolution*. Oxford University Press, Oxford.

- Wheeler W. 2001a. Homology and DNA sequence data. In: Wagner G.P. (ed.), *The Character Concept in Evolutionary Biology*, Academic Press, San Diego, pp. 303–317.
- Wheeler W. 2001b. Homology and the optimization of DNA sequence data. *Cladistics* 17: S1–S11.
- Wickler W. 1967. Vergleichende Verhaltensforschung und Phylogenetik. In: Heberer G. (ed.), *Die Evolution der Organismen*, 3. Auflage, Band I, G. Fischer, Stuttgart, pp. 420–508.
- Wiley E.O. 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. John Wiley & Sons, New York.
- Williams D.M. 2004. Homologues and homology, phenetics and cladistics: 150 years of progress. In: Williams D.M. and Forey P.L. (eds), *Milestones in Systematics*, CRC Press, Boca Raton, FL, pp. 191–224.
- Wilson R.A. 1999. Realism, essence, and kind: resuscitating species essentialism? In: Wilson R.A. (ed.), *Species. New Interdisciplinary Essays*, The MIT Press, Cambridge, MA, pp. 187–207.
- Wimsatt W.C. 1986. Developmental constraints, generative entrenchment and the innate-acquired distinction. In: Bechtel W. (ed.), *Integrating Scientific Disciplines*, Martinus Nijhoff, Dordrecht, pp. 185–208.
- Winther R.G. 2001. Varieties of modules: kinds, levels, origins, and behaviors. *J. Exp. Zool. (Mol. Dev. Evol.)* 291: 116–129.
- Zaher H. and Rieppel O. 2000. A brief history of snakes. *Herpetol. Rev.* 31: 73–76.