

1 Evolutionary Biology

2

3 ESSAY

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5 **Homology: Homeostatic Property Cluster Kinds in Systematics and Evolution**

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7 **Leandro C.S. Assis • Ingo Brigandt**

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9 L. C. S. Assis (author for correspondence)

10 Laboratório de Sistemática Vegetal, Departamento de Botânica, Universidade de São

11 Paulo, Rua do Matão 277, São Paulo, SP, 05508-090, Brazil, Tel: 55 11 3091 7545,

12 Fax: 55 11 3091 7547

13 e-mail: lcsassis@ib.usp.br

14

15 I. Brigandt

16 Department of Philosophy, University of Alberta, 2-40 Assiniboia Hall, Edmonton AB

17 T6G 2E7, Canada, Tel: +1 780-492-0623, Fax: +1 780-492-9160

18 e-mail: brigandt@ualberta.ca

19 **Abstract** Taxa and homologues can in our view be construed both as kinds and as
20 individuals. However, the conceptualization of taxa as natural kinds in the sense of
21 homeostatic property cluster kinds has been criticized by some systematists, as it seems
22 that even such kinds cannot evolve due to their being homeostatic. We reply by arguing
23 that the treatment of transformational and taxic homologies, respectively, as dynamic
24 and static aspects of the same homeostatic property cluster kind represents a good
25 perspective for supporting the conceptualization of taxa as kinds. The focus on a
26 phenomenon of homology based on causal processes (e.g., connectivity, activity-
27 function, genetics, inheritance, and modularity) and implying relationship with
28 modification yields a notion of natural kinds conforming to the phylogenetic-
29 evolutionary framework. Nevertheless, homeostatic property cluster kinds in taxonomic
30 and evolutionary practice must be rooted in the primacy of epistemological
31 classification (homology as observational properties) over metaphysical generalization
32 (series of transformation and common ancestry as unobservational processes). The
33 perspective of individuating characters exclusively by historical-transformational
34 independence instead of their developmental, structural, and functional independence
35 fails to yield a sufficient practical interplay between theory and observation. Purely
36 ontological and ostensional perspectives in evolution and phylogeny (e.g., an
37 ideographic character concept and PhyloCode's 'individualism' of clades) may be
38 pragmatically contested in the case of urgent issues in biodiversity research,
39 conservation, and systematics.

40

41 **Keywords** Characters • Individuals • Monophyly • Natural kinds • Phylogeny •
42 Similarity • Taxonomy • Transformational and taxic homology

43 **Introduction**

44

45 Taxa (hereafter, monophyletic groups) have been construed as *classes* (which have
46 members and are not spatio-temporally continuous and cohesive entities embedded in
47 the evolutionary contingency), or alternatively as *individuals* (which are wholes having
48 parts and are spatio-temporally continuous and cohesive entities embedded in the
49 evolutionary contingency; Rieppel, 2006). This seeming philosophical dichotomy
50 between classes and individuals has generated renewed approaches and debates in
51 contemporary systematics – theoretically, methodologically, and philosophically – such
52 as the elaboration of an ideographic character concept (Grant and Kluge, 2004) and the
53 clash between phylogenetic nomenclature and Linnaean taxonomy (Keller *et al.*, 2003;
54 Nixon *et al.*, 2003; Pleijel and Härlin, 2004; Wheeler, 2004; Rieppel, 2006; Cantino and
55 de Queiroz, 2007; and references therein).

56 However, this dichotomy is considered largely irrelevant for contemporary
57 systematics by those arguing that taxa can be conceptualized as *homeostatic property*
58 *cluster (HPC) kinds* (Keller *et al.*, 2003; Franz, 2005; Rieppel, 2005a, b, 2006, 2007a;
59 Assis, 2009). Originally introduced by Richard Boyd (1991, 1999), the HPC construal
60 of kinds attempts to reconcile the fact that kinds in the biological and social sciences are
61 typically heterogeneous and cannot be defined by necessary or sufficient conditions
62 (essences, which define classes), with the observation that such categories are not
63 formed in an arbitrary fashion and epistemically permit scientific generalizations and
64 explanations (Wilson *et al.*, 2009). The approach suggests that a kind is ontologically
65 characterized by a *property cluster*, i.e., a larger set of properties that exhibit a relevant
66 degree of correlation, where each kind member possesses several (though usually not

67 all) of these properties, and no single property must necessarily be shared by all kind
68 members. Such a kind is a natural kind (rather than an arbitrary collection of objects) if
69 the clustering of the various properties is due to underlying causal processes, so-called
70 *homeostatic processes*.

71 In the context of phylogenetic systematics, the property cluster characterizing a taxon
72 consists of taxic homologies or synapomorphies (Keller *et al.*, 2003; Franz, 2005;
73 Rieppel, 2006). Common descent (involving reproduction across generations) is here
74 the ‘homeostatic process’ that accounts for the clustering of these characters and the fact
75 that phylogenetic classifications have a rich information content, e.g., “the
76 characterizations of 38,000 kinds of spiders by their spinnerets (silk-producing glands),
77 or of 250,000 kinds of flowering plants by their endosperm (resulting from the process
78 of double fertilization)” (Franz, 2005, p. 497). Thus, homeostatic property cluster kinds
79 are “scientific categories posited by our theories as epistemological devices; insofar as
80 they have ontological status, it is as features of the ways in which causal structures in
81 the world interact with our classificatory practices in such a way as to support reliable
82 induction and explanation” (Keller *et al.*, 2003, p. 102). This thesis is claimed to allow
83 natural kinds to be historically delimited, because of the reference to common ancestry
84 in the case of taxa (Keller *et al.*, 2003; Rieppel, 2007a, b).

85 A few have suggested that there is no incompatibility between a taxon being
86 construed both as a kind and as an individual (Dupré, 1999; LaPorte, 2004; Brigandt,
87 2009), for both constructions are context sensitive. However, the conceptualization of
88 taxa as natural kinds even in the sense of homeostatic property cluster kinds has been
89 criticized by some systematists (e.g., Kluge, 2003; Grant and Kluge, 2004), as it seems
90 that even such kinds cannot evolve due to their being based on homeostatic processes.

91 However, we reply by arguing that the treatment of transformational and taxic
92 homologies, respectively, as dynamic and static aspects of the same homeostatic
93 property cluster kind offers a good perspective for supporting the conceptualization of
94 taxa as kinds. The focus on a phenomenon of homology (i.e., the relation of
95 correspondence between parts of two or more organisms) based on causal processes
96 (e.g., topology, connectivity, activity-function, ontogeny, genetics, inheritance, and
97 modularity in development and evolution) and implying relationship with modification
98 yields a notion of natural kinds conforming to the phylogenetic-evolutionary
99 framework.

100 While assuming that ontologically speaking an individual and a kinds approach are
101 consistent, we focus on articulating how to construe taxa and in particular homologues
102 as HPC kinds, because some still argue that this is impossible, and – more importantly –
103 because we explore new perspectives, showing how the HPC approach motivates and
104 successfully addresses them. This paper recommends the notion of HPC kinds for its
105 heuristic and theoretical fruitfulness in tying taxic to transformational homology,
106 combining empirical-pragmatic and theoretical-explanatory aims in taxonomy and
107 evolutionary biology, and making accounts of homology germane to a plethora of
108 issues. This embraces evolvability, adaptation, diversification, research on the
109 developmental-functional make-up of organisms, the phylogeny-taxonomy link,
110 biodiversity and conservation policies, as well as the continuity of philosophy with
111 empirical science. We do not maintain that the individuals perspective is wrong, but
112 challenge it on the grounds that it has not previously motivated the indispensable issues
113 in systematics and evolution we explore in these pages.

114

115 **From properties of classification to events of generalization**

116

117 Some metaphysically realist systematists influenced by the purely ontological
118 conception of species and monophyletic groups as individuals such as Grant and Kluge
119 (2004, p. 25) have criticized the construal of character states as properties: “character-
120 states have generally been conceptualized as properties (attributes, features), which
121 logically denies their ability to transform or evolve, since properties are class concepts
122 and, as such, immutable.” Instead they propose an ideographic character concept: “as
123 transformation series, characters are historical individuals akin to species and clades”
124 (Grant and Kluge, 2004, p. 23). Accordingly, character states are “*the least inclusive*
125 *historical individuals that result from heritable transformational events*” (Grant and
126 Kluge, 2004, p. 26; emphasis in original). And “because the basic or fundamental unit
127 in phylogenetic inference is the transformation event, the relevant independent parts of
128 organisms are those that have undergone independent, heritable transformation events.
129 What matters in individuating character-states (and more inclusive transformation
130 series), therefore, is not the structural, developmental, or functional independence of a
131 part, but its historical/transformational independence” (Grant and Kluge, 2004, p. 26;
132 contra Rieppel and Kearney, 2002). Hence, a strict ontological character concept is
133 proposed that represents the primacy of generalization (e.g., an explanatory theory of
134 historical singular processes) over classification (e.g., contextual patterns of
135 membership relations by properties) in phylogenetic systematics (cf. Rieppel, 2004).
136 Correspondingly, Grant and Kluge (2004, p. 25) reject the possibility of construing
137 species as kinds, even as homeostatic property cluster kinds, claiming that “in being
138 homeostatic, such kinds cannot evolve.”

139 However, when assuming that a character, as a relation of ‘sameness’ captures the
140 notion of transformational (e.g., the homologues A and A’) and taxic homologies (e.g.,
141 A’), the tenet of Kluge (2003) and Grant and Kluge (2004) about the non-phylogenetic-
142 evolutionary nature of HPC kinds fails to meet its target, because a hypothesis of
143 transformational and taxic homologies – as we will see below – are critical for making
144 the idea that homologies and taxa are HPC kinds conform to an evolutionary
145 framework. An important point is that the fundamentals of transformational and taxic
146 homologies in phylogenetic theory and practice are not strictly ontological like an
147 ideographic character concept is. They are also epistemological and, as such, instantiate
148 a relation of classification (or knowledge of observational facts) to generalization (or
149 explanatory theories of unobservable phenomena). In fact, conjectures of
150 transformational and taxic homologies are firstly established by the empirical-
151 contextual delineation of characters (i.e., by similarity or correspondence) with their
152 subsequent polarization (i.e., definition of relatively correspondent plesiomorphic and
153 apomorphic character states within characters onto the phylogenetic hierarchy; Bryant,
154 2001) by cladogram rooting (see Grant *et al.*, 2006, as an example of these empirical
155 and logical approaches). And only after the hierarchical construction the evolutionary
156 explanation is carried out. It is in this way that the conceptualization of taxa as HPC
157 natural kinds and their accommodation to evolutionary properties and events (contra
158 Grant and Kluge, 2004) must be further investigated through the treatment of
159 transformational and taxic homologies as dynamic and static aspects of a homology, and
160 thus as different aspects of the same HPC kind, which thereby permits phylogenetic
161 relatedness and modification.

162

163 **Transformational and taxic homologies, modification and homeostasis**

164

165 It turns out to be erroneous to assume (as Kluge, 2003 and Grant and Kluge, 2004 do)
166 that an entity whose identity is based on homeostatic processes – at least as this notion
167 is used in the HPC construal of kinds – is essentially unchanging in most of its features.
168 Rieppel (2005a, p. 482) discusses the meaning of homeostasis as “the maintenance of a
169 dynamically stable internal environment in an open system.” In this way, an individual
170 organism is a dynamically stable system that keeps many properties during its life time,
171 despite undergoing ontogenetic development as change in other properties (e.g., its
172 series of semaphoronts; see Hennig, 1966). There are ‘homeostatic’ processes that
173 explain both why the individual keeps its identity across time and can change as an
174 integrated entity, including self-maintenance as a variety of cellular, physiological, and
175 behavioral processes (Wagner and Laubichler, 2001), phenotypic plasticity and
176 developmental constraints (Rieppel, 2005a, b).

177 The same idea applies to a species taxon construed as an HPC kind (Wilson *et al.*,
178 2009). Conspecifics share many features in certain combinations – the cluster of
179 properties characterizing an HPC kind. This correlation and distribution of properties is
180 explained by processes accounting for species cohesion, as laid out by different species
181 concepts. One such process is gene flow. Gene flow across conspecifics is not at all
182 incompatible with evolutionary change; in fact, it accounts for why a species changes *as*
183 *a coherent unit*, should it change due to natural selection and other influences, since
184 change in some populations is transmitted via gene flow to the rest of the species. Thus,
185 the so-called ‘homeostatic’ processes account for why the members of an HPC kind
186 existing at the same point in time exhibit similarities, and why change typically affects

187 all kind members, so that the kind changes as a unit. Gene flow and the ability to
188 interbreed are relational rather than intrinsic properties, but the HPC approach permits
189 such properties and considers them as important for the identity of biological kinds,
190 including the relational property of common descent.

191 This brings us to the ability of characters to evolve, as emphasized by Grant and
192 Kluge (2004). An important issue for construing characters as HPC kinds consistent
193 with an evolutionary framework is the relation between ontogeny, inheritance, and
194 phylogeny, where the concepts of homologue and homology as well as semaphoront
195 and ‘complex semaphoront’ are fundamental. A homologue is “a part of an organism”
196 and homology is “a phylogenetic relationship between parts, or homologues of different
197 organisms” (Nelson, 1994, p. 104). According to Hennig (1966, p. 65), “the
198 semaphoront corresponds to the individual in a certain, theoretically infinitely small,
199 time span of its life, during which it can be considered unchangeable,” whereas “a
200 ‘semaphoront complex’ can be constructed by aspect fusion of several aspect continua
201 representing the same organism at different ontogenetic stages” (Rieppel, 2003, p. 172).
202 As an organism is contextually composed of parts (homologues), each such part,
203 throughout its ontogenetic stages, is characterized by a complex semaphoront.
204 Developmental and genetic constraints act in the construction of the ‘semaphoront
205 complex’ as a dynamic entity integrated by homeostatic processes, so that each one of
206 its semaphoronts corresponds to a static, ‘unchangeable’ stage in a certain time span of
207 the organism’s life. “But just as a ‘semaphoront complex’ [i.e., an ontogenetic unity]
208 can be constructed for a single organism, so it can also be constructed by aspect fusion
209 for species and higher taxa” (Rieppel, 2003, p. 172). As such, taxa can be
210 conceptualized as “phylogenetic relationships [...] of ontogenetic parts of life” (Nelson,

211 1989a, p. 279), so that these parts are homologues (e.g., A or A') of a character in
212 different organisms, and these homologues, in the phylogenetic-evolutionary hierarchy,
213 capture relations of transformational and taxic homologies.

214 The *transformational* perspective on homology, i.e., the relation between different
215 states of a character found in two or more organisms, is concerned with change (e.g.,
216 $A \rightarrow A'$) and need not imply grouping (Patterson, 1982; Rieppel, 1988). The *taxic*
217 perspective, i.e., the relation between identical, apomorphic character states shared by
218 two or more organisms, is concerned with common ancestry and grouping (e.g., A'),
219 being operationally established by the overall congruence of characters in a hierarchy
220 (Patterson, 1982) (i.e., a set-theoretical notion irrespective of causal phenomena, unless
221 it is qualified by causal-contextual efficacious properties; Rieppel, 2004). The
222 transformational account with its focus on evolutionary change represents the *dynamic*
223 aspect of the HPC kind (i.e., a phenomenon of homology), whereas the taxic account
224 with its relation to the monophyly and classification of groups represents the *static*
225 aspect of the same HPC kind.

226 This is possible as there are different properties ontologically associated with an
227 HPC kind, some of which are more static, while others are more dynamic. Some of
228 these properties are causally more basic, while others are the effects of the former; some
229 are non-observational, while others are observable (Brigandt, 2009). In the case of a
230 higher taxon as an HPC kind, descent from a particular ancestral species is a (non-
231 observational) causally basic feature that *explains* why the (observable) apomorphies of
232 the taxa members – some further properties of the HPC cluster – are shared, and
233 common ancestry is a property shared by taxa members that permits other properties
234 (characters) to change and evolve. A species taxon construed as an HPC kind is

235 ontologically characterized by many features that stand in complex and reciprocal
236 causal relations, e.g., genetic properties of individuals, their phenotypic features, gene
237 flow and the ability to interbreed, ecological competition, and developmental
238 constraints (Wilson *et al.*, 2009). Rieppel (2008) emphasizes that a particular scientific
239 approach is typically interested in only certain aspects tied to a kind, be it phylogenetic,
240 developmental, functional, anatomical, or ecological features. Indeed, there are different
241 species concepts based on different biological features and operational approaches (see
242 Wheeler and Meier, 2000; and references therein). Yet the fact that only some features
243 of a taxon or a homology are of epistemological or pragmatic interest in a certain
244 scientific context does not entail that there are no other features ontologically tied to this
245 entity that may be relevant given other scientific interests; and the HPC approach
246 explains how different perspectives on a kind can be consistent and related.

247 In the case of a homology (a character across generations) as an HPC kind, certain
248 genetic-developmental properties of the character permit that it can be inherited across
249 generations and undergo change of state while remaining the same morphological unit
250 (Wagner, 1996, 2001; Jamniczky, 2008). Wagner (2007) presents evidence that the
251 identity of a character is established by *certain* gene regulatory networks, which have
252 been stable across evolutionary change (so that the character is present in several extant
253 species), while *other* genes have evolved leading to this character taking different states
254 in ancestral and extant species. This illustrates how different features are tied to an HPC
255 kind – some of which are more evolutionary stable, some of which are subject to change
256 – and that a character construed as an HPC kind can evolve (contra Grant and Kluge,
257 2004).

258 Grant and Kluge (2004) restrict the notion of homology to the transformational

259 account. But by regarding homology as both a homeostatic property cluster kind and a
260 relation between parts, we conceive homology within a broader scope. In this manner,
261 the same phenomenon of homology (as an HPC kind) encompasses the *transformative-*
262 *dynamic* aspect of homologues (e.g., $A \rightarrow A'$) and the *taxic-static* aspect of one such
263 homologue or character state (e.g., A') shared ontologically by all descendants and their
264 most recent common ancestry. Monophyly integrated with developmental and genetic
265 constraints are the homeostatic processes that determine a taxon's boundary (Brigandt,
266 2009). As taxic homologies are responsible for the identification and classification of
267 monophyletic groups, their importance over transformational homologies has been
268 pragmatically endorsed in phylogenetic theory and practice (see Patterson, 1982;
269 Rieppel, 1988; de Pinna, 1991; Brower and Schawaroch, 1996). Criticisms have been
270 made regarding the ontological nature of a transformation series (see Rieppel, 1988).
271 But whereas most of the papers concerned with the integration of the theory of natural
272 kinds and phylogenetic systematics focus on the treatment of taxic homologies (or
273 synapomorphies) as HPC kinds (e.g., Keller *et al.*, 2003; Franz, 2005; Rieppel, 2005a,
274 b, 2006), transformational homologies – the most critical feature to dispel the idea that
275 an HPC kind cannot evolve – have only recently been considered (see Brigandt, 2007,
276 2009).

277 Since a taxic homology, i.e., the apomorphic homologue that identifies a
278 phylogenetic relationship as a taxon, is included in a series of transformations, it is an
279 ongoing phenomenon in the world (Keller *et al.*, 2003). As such, it is subject to
280 modification. Moreover, by regarding the causal-contextual properties (or tokens) that
281 define a taxon (qua natural kind) as embedded in the evolutionary contingency, one has
282 to expect the occurrence of some reversions (i.e., the appearance of an apomorphic

283 condition within a natural kind, so that this condition is similar to the plesiomorphic
284 condition found at a more inclusive level in which that natural kind is contained) and
285 derivations (new character states). Other homologues (as HPC kinds) found in the taxon
286 are also subject to change and consequently promote diversification and novelty within
287 it. For instance, in the phylogeny of Reptilia, the position of turtles (Testudines,
288 classically considered anapsids) within Diapsida reveals that the lack of holes behind
289 the eye socket is – following the phylogenetic levels of universality – a reversion in
290 Reptilia, an apomorphic or derivate condition in Diapsida (which is phylogenetically
291 circumscribed by the presence of two holes behind the eye socket), and a synapomorphy
292 of Testudines (see Rieppel, 1999; and references therein). In this way, lack and presence
293 of holes behind the eye socket are states that characterize the skull of Diapsida and
294 Reptilia as a causal, historical, and dynamic unit integrated by homeostatic processes,
295 which is related to certain events of origin and diversification within these groups.

296 Since the notion of homologies as HPC kinds embraces relationship with
297 modification, it is germane to evolvability, “the capacity of a developmental system to
298 evolve” (Hendrikse *et al.*, 2007, p. 394). In other words, evolvability “is a disposition
299 that an organism and its homologues can possess” (Brigandt, 2007, p. 712). In line with
300 this, morphological organization into distinct homologues, developmental constraints,
301 and modularity explain evolvability (Yang, 2001; Brigandt, 2007; Jamniczky, 2008).
302 This perspective plus the theory of HPC kinds can also be used in studies of
303 diversification, selection, and adaptation (e.g., Yang, 2001). According to Brigandt
304 (2007), in contrast to what has often been assumed, developmental constraints and
305 selection are not antagonistic forces, but complementary. For developmental constraints
306 are related to the developmental generation and evolutionary maintenance of

307 homologues as units of morphological variation across generations (identity of a
308 morphological unit despite its phenotypic change), while natural selection subsequently
309 operates on the produced variation (resulting in character transformation).

310 In fact, Yang (2001) argues that developmental aspects of juveniles and adults stages
311 of hemi- and holometabolous insects can be conceived of as modules (or causal
312 properties) of evolutionary change relative to events of diversification and adaptation.
313 The author highlights that, based on these features, Holometabola was found to have a
314 significant rate of diversification when compared to its sister-group Eumetabola
315 (traditionally a hemimetabolous). In addition, Yang (2001) shows that the characters in
316 more modular monophyletic groups partake in greater levels of variation due to their
317 independence. This may imply that developmental constraints and selection act
318 complementarily in the static and dynamic aspects of these insects' parts or modules
319 (i.e., homologues as a HPC kinds), and consequently, in their events of origin and
320 diversification.

321

322 **Similarity again and forever**

323

324 Identical or similar character states in a monophyletic group are *one* aspect of an HPC
325 kind. However, Ereshefsky (2007, p. 296) charges that "HPC's emphasis on similarity
326 is at odds with phylogenetic approaches to taxonomy." We reply by pointing out that
327 apart from members of the same HPC kind sharing certain internal features, there are
328 also *relations to members of other kinds*, which in this case account for a character (a
329 homology) being a unit of evolutionary transformation. Some of the genetic-
330 developmental properties of a morphological structure (or developmental module)

331 pertain to how this structure is partially developmentally dissociated from other
332 structures, so that across generations it can vary and evolve largely independently of
333 other structures (Brigandt, 2009). Among other things, the growing literature on
334 modularity works towards an explanation of how structures that exhibit some
335 developmental and functional relations can be sufficiently dissociated so as to permit
336 morphological change (von Dassow and Munro, 1999; Schlosser and Wagner, 2004;
337 Rieppel, 2005b). What makes a character a phylogenetic unit is its ability to evolve
338 independently of other characters (Wagner and Laubichler, 2001). Construing a
339 character as an HPC kind is not only consistent with a character being able to evolve,
340 but some of the developmental relations and dissociations w.r.t. other characters – an
341 aspect of the HPC kind in addition to internal similarities – explain this ability to evolve
342 in a character-by-character fashion (Brigandt, 2007).

343 To be sure, the relations of correspondence among different character states (i.e.,
344 transformational homology as a dynamic aspect of an HPC unit) and the same
345 homologues (i.e., taxic homology as a static aspect of an HPC unit) are causally and
346 contextually evidenced according to heterogeneous criteria of comparative biology, as a
347 way of seeing the biological world whereby similarity / correspondence between parts
348 of organisms (homologues) is empirically and theoretically justified by activity-
349 function, ontogeny, genetics, inheritance, and modularity in development and evolution.
350 Yet it is important to bear in mind that these developmental, functional, and modular
351 phenomena are largely unexplored for characters in phylogenetic inferences, and that
352 these relations need to be established by classical approaches to comparative biology,
353 such as topological relations and/or connectivity (the resemblance in position and
354 arrangement between structures) (Rieppel, 1988; Rieppel and Kearney, 2002; Kearney

355 and Rieppel, 2006). These two classical criteria of correspondence are conventionally
356 and more or less successfully used throughout the systematic and comparative endeavor
357 as the panacea for solving problems of the common origin of homologues (Rieppel and
358 Kearney, 2002; Kearney and Rieppel, 2006). Indeed, as monophyly is not immediately
359 given, it must be parasitic on homology (see Dupré, 1981; Nelson, 1994; Rieppel, 2003,
360 2006). Taxa and characters delineation is empirical-contextual (Franz, 2005).

361 Following the thesis of individualism, Grant & Kluge (2004) stress that
362 developmental independence is not fundamental for individuating historical character-
363 states in phylogenetic systematics, whereas Ghiselin (2005) realizes that homologies as
364 historical entities / individuals are grounded among other things in developmental
365 processes. In the context of an empirical-contextual discourse, homologies and taxa as
366 individuals are levels of biological organization with asymmetric construction.
367 Homologies can be construed by substantial knowledge (see Ghiselin, 2005), but taxa
368 cannot. Specific parts or processes (e.g., developmental and taxic homologies) do not
369 define taxa as individuals, for these are whole-part relations. Hence, the individualism
370 of taxa cannot be grounded in data matrix and cladogram construction (contra Cantino
371 and de Queiroz, 2007; Ereshefsky, 2007). The only way of making reference to their
372 individualistic monophyly is by stipulation plus ostensional indication (i.e., by ‘pointing
373 out’ paradigmatic exemplars of a taxon without any empirical-contextual knowledge
374 about its referent; cf. Rieppel, 2007b, 2008). Accordingly, the perspective of
375 individuating characters exclusively by historical-transformational independence
376 instead of a part’s developmental, structural, and functional independence (e.g., Grant
377 and Kluge, 2004) is, in the language of systematics, virtually devoid of any practical
378 interplay between theory and observation.

379

380

381 **Conclusions**

382

383 Taxa and homologues can in our view be construed both as kinds and as individuals
384 depending on the context of a certain scope of discourse. Consequently, both
385 constructions face the problem of instantiating theoretical-causal entities and the terms
386 that name them w.r.t. two indispensable and reciprocal approaches – the
387 epistemological knowledge of systematics and the metaphysical phenomenon of
388 evolution. A successful perspective for making the theory of homeostatic property
389 cluster kinds conform to phylogenetic systematics depends upon the treatment of
390 transformational and taxic homologies, respectively, as dynamic and static aspects of
391 the same phenomenon of homology (i.e., as modification and relationship in a
392 hierarchical reconstruction) grounded in efficacious causal-contextual properties. These
393 properties capture relations of similarity (in language by predicates; Rieppel, 2007b),
394 which are fundamental for phylogenetic reconstructions, classifications of biodiversity,
395 and related approaches (Assis, 2009). The transformational account of homology
396 focuses on how a character is inherited and gradually modified through generations and
397 species, while the taxic approach focuses on a split in a lineage (formation of different
398 taxa) and the resulting marked differences between extant species of different taxa.

399 An adequate notion of HPC kinds establishes an epistemological and ontological
400 basis for the naturalization of the Linnaean taxonomy – as a verbal reference system for
401 systematics – grounded in Hennigian phylogenetic systematics – as a general reference
402 system for systematics (Hennig, 1966) –, and the consequent replacement of

403 paraphyletic groups or nominal kinds by monophyletic groups or natural kinds (Rieppel,
404 2006). Nevertheless, the conceptualization of taxa as classes, in Linnaean taxonomy,
405 and individuals, in Hennigian phylogenetics, can fruitfully be replaced by a construal of
406 taxa as natural kinds (Keller *et al.*, 2003; Rieppel, 2006). For in addition to theoretical-
407 explanatory aims HPC natural kinds satisfy simultaneously historical, empirical, and
408 methodological demands of contemporary systematics. Thus, we recommend the HPC
409 approach because of its heuristic fruitfulness for a variety of issues, not because it
410 would metaphysically exclude the individualism approach.

411 Even though species and higher taxa are pragmatically and contextually
412 circumscribed in different ways (i.e., there are different species concepts, and higher
413 taxa are phylogenetically delimited by synapomorphies distributed in a cladogram),
414 their ontological status in the systematics-evolution link is the same – they can be
415 construed as HPC natural kinds. Therefore, it is false to assume an empirical difference
416 between species and higher taxa as units of systematics and evolution (see Nelson,
417 1989b). Both are contextually delineated based on (relational) properties and
418 homeostatic processes at distinct levels of universality.

419 Historically, extensional and intensional definitions – empirically based accounts of
420 characters, homologues, and taxa – when compared to an ostensional individuation or
421 baptism (cf. Rieppel, 2007b), have provided great conceptual advances in our
422 epistemological and ontological schemata in the context of systematics and the
423 evolution of biodiversity. Substantial knowledge is consequently required for
424 homologies' construal both as kinds and as individuals. In contrast, Grant and Kluge's
425 (2004) metaphysical realism about individuals and characters does not provide an
426 advancement in our knowledge of observational beliefs, concepts and terms relative to

427 the language of systematics and everyday life. At the end of the day, their ideographic
428 character concept has merely ontological status that fails to do justice to the essential
429 continuity of philosophy with empirical science.

430 As homeostatic property cluster kinds in systematics, evolution, and biodiversity
431 research are fundamentally and historically rooted in the epistemological primacy of
432 classification (e.g., homology and taxonomic hierarchy) over generalization (e.g., series
433 of transformation and common ancestry) (see Rieppel, 2004), it emerges as an
434 appropriate approach in an attempt to provide that continuity. As a result, a purely
435 ontological assumption, stipulation, and ostension in evolution and phylogeny, e.g., the
436 ideographic character concept (Grant and Kluge, 2004) and the ‘individualism’ of
437 clades as endorsed by the PhyloCode (Cantino and de Queiroz, 2007; see also
438 Ereshefsky, 2007), may be pragmatically contested in the case of urgent issues in
439 contemporary systematics. These include the renaissance of taxonomy and comparative
440 morphology, homology assessment, as well as the crisis, knowledge (e.g., faunas, floras,
441 monographs, and revisions), phylogenetic classification, and the conservation of
442 biodiversity (Wheeler, 2004; de Carvalho *et al.*, 2008; Assis, 2009).

443

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445

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