Cladotypic Taxonomy Revisited

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> Abstract

New propositions are made in order to implement the cladotypic taxonomic system. The term 'taxon' designates *metapopulation lineages that evolved from a unique metapopulation lineage*. In other words, a taxon is composed of a species that experienced a cladogenesis event, and all its descendants. A new formulation for the definition of particular taxa is proposed: a taxon is a *species that evolved from the (segments of) metapopulation lineage in which the character state* [defining character state], *as exhibited by* [species 1] *and* [species 2], *has been acquired*. An assumption on the polarity of type character states is developed in order to allow the falsification of taxa defined by symplesiomorphies. It is based on a new sense given to 'adelphospecies' (or adelpholineage) and to the new concept of 'amitaspecies' (or amitalineage). The adelphospecies is understood as the closest sister-species of a taxon T to which the character involved in the definition of T is applicable. As a consequence of the definition of T, the adelphospecies exhibits a character state different from that exhibited by T. The amitaspecies is the closest sister-species of the taxon including T and its adelphospecies. The assumption of polarity takes the form: *an amitaspecies can be identified and, regarding the character involved in the definition, it exhibits a character state different from that exhibited by the taxon*. Finally a practical version of the isolation assumption is proposed.

1.   Introduction

A taxonomic system alternative to the Linnaean and the phylogenetic ones was proposed recently (BÉTHOUX 2007a). As currently elaborated, the definition of a taxon necessitates the designation of two type-specimens (cladotypes), belonging to different species, and exhibiting a similar character state suggesting common ancestry. Formulation of the character state takes part in the taxon definition. As currently developed the system relies on two assumptions that are '*the character state typified by cladotypes is homologous in individuals that are designated as cladotypes*' (referred to as the homology assumption thereafter) and '*cohesion mechanisms isolated individuals exhibiting the type character state from those that do not*' (isolation assumption). Therefore, taxa are falsifiable hypotheses of common ancestry (or hypotheses the likelihood of which can be estimated), based on presumed homologies.

Application of the system revealed the necessity of a formal frame for the adaptation of taxon names erected under the Linnaean system, and highlighted the advantage of abandoning taxa ranks at all taxonomic levels (BÉTHOUX 2007b; in prep.). Nonetheless it appears that the main assumptions that allow the falsification of taxon validity are to be reconsidered. In the following I propose a new formulation of particular taxon definitions, develop an assumption on the polarity of the type character state, and discuss the practical value of the isolation assumption. First of all, a set of definitions and conventions is provided.

2.   Definitions and conventions

A taxon is considered as a *group of metapopulation lineages that evolved from a single metapopulation lineage, forming altogether a single metapopulation lineage*. This definition is derived from the species definition of DE QUEIROZ (2005a, b). The proposed taxon definition is then equivalent to *a group of species that evolved from a unique species*. A taxon is a metapopulation lineage that underwent a cladogenesis event. A species is simply a metapopulation lineage, whether it underwent cladogenesis events or not. With this view

taxa are particular species that underwent cladogenesis events. Then 'taxon' is a subset of the 'species' category. A species that undergoes a cladogenesis event results into three lineages: the two daughter-species, and the two daughter-species and their parent-species taken altogether (considered as a whole as a unique lineage). This view is consistent with the paradigm initiated and developed by DARWIN (1858, 1859), WALLACE (1858), among others, under which each subset of living species share a unique ancestor, which has been a unique species at some point.

A simple example will demonstrate that this new position is grounded. Individuals belonging to the (Linnean class) Mammalia form a separately evolving (meta-)population lineage, and a reproductively isolated, ecologically differentiated, and monophyletic group. The same characteristics apply to the (Linnean class) Aces, which forms a (meta-)population lineage evolving separately from Mammalia, which individuals are reproductively isolated from those belonging to Mammalia, which individuals are ecologically differentiated from those belonging to Mammalia, and which constitutes a monophyletic group distinct from Mammalia. Therefore the taxa Mammalia and Aves comply with the general species definition of De Queiroz (2005a, b), but also with the ecological species definition and the phylogenetic species definition. Mammalia and Aves do not totally comply with the biological species definition: though individuals belonging to Mammalia are reproductively isolated from those belonging to Aves, Mammalia as a whole is not composed of individuals sharing interbreeding potential, neither is Aves. This is because these entities underwent cladogenesis events and this is their only difference with species. Therefore they could be considered as species that underwent cladogenesis events.

The new proposition is inconsistent with the views of HENNIG (1966), who considers that an ancestral species does not exist anymore once it experienced a cladogenesis event. On the contrary, I consider that an ancestral metapopulation lineage / ancestral-species exists if at least one of its descendants exists. A given metapopulation lineage can have a limited time duration resulting from the extinction of all of its inner metapopulation lineages, but not as the result of experiencing a cladogenesis event. Based on the position that species have a duration in time limited by two cladogenesis events, HENNIG (1966) considers that all supra-individual categories (i.e. species and taxa) are distinct "parts", hence are individuals. Following my proposition, taxa can include taxa (i.e. metapopulation lineages can include metapopulation lineages), therefore they cannot be individuals.

Considering taxa as a particular case of species is at odds with the traditional viewpoint, under which species are a particular category of taxa. This notion is an outcome of the century-old use of a ranked taxonomy, under which species are entities to which the lowest rank is assigned. This inconsistency demonstrates that ranked taxonomy does not appropriately accommodate with the paradigm mentioned above. Under cladotypic taxonomy, the taxonomic address that precedes a uninominal species name must be understood as a list of metapopulation lineages that experienced cladogenesis and from which derived a given ultimate species (see DAYRAT et al. 2004; BÉTHOUX 2007b).

The concept of homology, which is fundamental in the homology assumption, needs to be better outlined. A character state is said homologous in two species if it is shared by the closest common ancestor of these species and by all lineages from which these species evolved directly. In case of polarization ambiguity regarding lineages from which these species evolved, I suggest that a character state is considered as homologous until an unambiguous evidence of occurrence of a different character state in lineages from which directly evolved one (or both) of the species under scrutiny is provided. This concept of homology implies that primary homology, as understood by DE PINNA (1991), is established for the character state.

I propose to use the word 'adelphospecies' (based on 'adelphe', sister in Greek; or adelpholineage) in a new sense. Considering a taxon T defined under cladotypic taxonomy, by definition the closest sister-species (or brother-lineage) of T exhibits a character state different from that exhibited by T. This species is termed 'adelphospecies' (i.e. the closest sister-species or brother-lineage of the lineage in which the defining character state of T has been acquired). The character involved in the definition of T is to be applicable to the adelphospecies. Otherwise the adelphospecies cannot be identified. I propose the term 'amitaspecies' (or amitalineage) for the closest sister-species (or lineage) of the taxon including T and its adelphospecies (from 'amita', aunt in Latin). Following a hierarchical formulation, these designations can be depicted as [amitaspecies (adelphospecies, taxon)] {or [amitalineage (adelpholineage, taxon)]}. While the adelphospecies is identified after a character state and its relation to T, the amitaspecies is identified only after its relation to T and the adelphospecies of T. The terms adelphospecies and amitaspecies can be used to make reference to relatives of cladotypic species taken isolated.

All erected names, designating a valid taxon or not, are part of the nomenclature. All names that are considered as valid are part of the taxonomy. Nomenclatural names could be written in regular letter, taxonomic names in italics. The general use is to write taxon names with a capital first letter, and names of species that underwent no cladogenesis event (i.e. specific 'epithet' in Linnean taxonomy) without a capital letter, which I propose to follow.
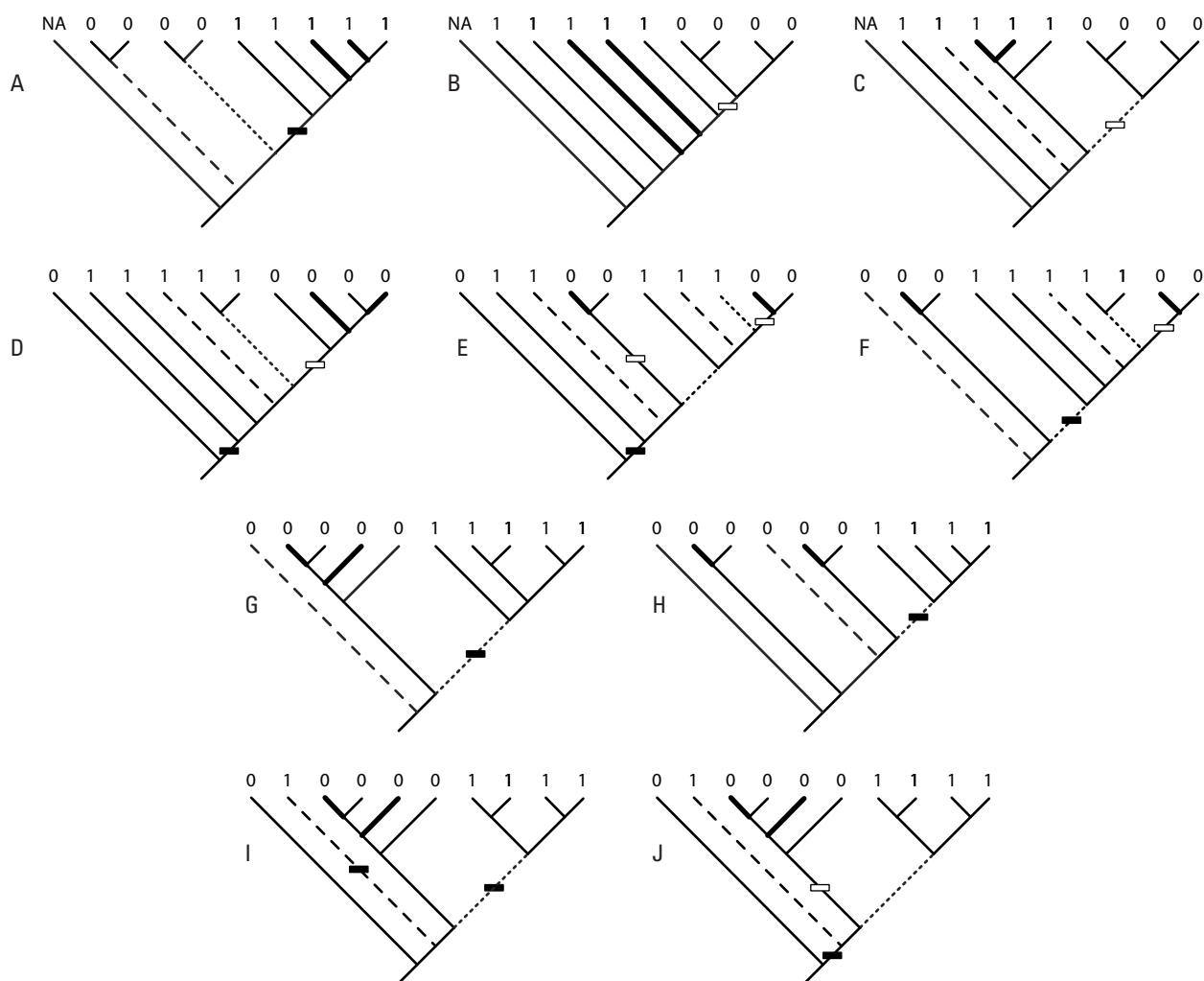
Fig. 1. Possible cases of taxon status (cladotypic species are indicated by bold branches; adelphospecies are indicated by dotted lines; amitaspecies are indicated by dashed lines; black rectangles indicate transformation from the state 0 to 1; white rectangles indicate transformation from the state 1 to 0). In case of a valid taxon definition, the defining character state is homologous in cladotypic species, and the amitaspecies exhibits a different character state; the name refers to a synapophyletic assemblage (A). If no adelphospecies can be identified, the taxon is defined on a symplesiomorphy and is invalid; the name refers to a symplesiophyletic assemblage (B). If an adelphospecies can be identified but exhibits the same character state as cladotypic species, the taxon is defined on a symplesiomorphy and is invalid; the name refers to a symplesiophyletic assemblage (C). In case of taxon definition based on a reversion, the taxon is valid if cladotypic species acquired the defining character state from a common ancestor, and if the defining character state is not shared by the amitaspecies; the name refers to a synapophyletic assemblage (D). A taxon is invalid if cladotypic species acquired the defining character state from different ancestors; the name refers to a diapophyletic assemblage (E). A taxon is invalid if the defining character state is a plesiomorphy in one of the cladotypic species (if identifiable, its amitaspecies shares the defining character state), and secondarily reversed in the other cladotypic species (its amitaspecies does not share the defining character state); the name refers to an asymphyletic assemblage (F). A taxon is invalid if cladotypic species belong to a monophyletic clade which amitaspecies shares the defining character state; the name refers to a symplesiophyletic assemblage (G). A taxon is invalid if no amitaspecies common to both cladotypic species can be identified; the name refers to a symplesiophyletic assemblage (H). Until an unambiguous evidence of homoplastic distribution of the defining character state involving cladotypic species is provided, a taxon is considered as valid; the name refers to a synapophyletic assemblage (F,G).

3. Formulation of particular taxon definitions

The current proposition for cladotypic definition of a taxon takes the form '*Species related to* [species 1] *and* [species 2] *by the sharing of* [defining character state]'

(BÉTHOUX 2007a). A rather evident problem is the assignment of species exhibiting a character state different but derived with respect to the defining character state. This could be the case of a reversion (Fig. 1D). Positing a taxon defined by the lack of wings typified by two grylloblattodean insects, it is highly probable that the adelphospecies and amitaspecies of this taxon

exhibit wings (i.e. grylloblattodean and wingless relatives arguably derived from winged insects). Under the current scheme the assignment of members of this taxon to *Pterygota* (winged insects) happens to be problematic. Therefore, I propose a different formulation, derived from the general taxon definition mentioned above: a particular taxon is defined as *species that evolved from the (segments of) metapopulation lineage in which the character state* [defining character state], *as exhibited by* [species 1] *and* [species 2], *has been acquired*. Assigning grylloblattodeans and wingless putative relatives to *Pterygota* is consistent with this new formulation.

4.   Polarity assumption

Mention of character state polarity is not explicit in the sense of homology proposed above. Therefore, under the current frame, a definition could be based on a character state which could be a symplesiomorphy. If so, falsification of the validity of a taxon could be problematic. This problem will be illustrated by two cases: the case of a taxon defined on a presumed synapomorphy that turns out to be a (sym)plesiomorphy, and the case of a taxon defined on a presumed reversion that turns out to be a (sym)plesiomorphy. In both cases it will be argued that the new assumption *an amitaspecies can be identified and, regarding the character involved in the definition, it exhibits a character state different from that exhibited by the taxon* allows a falsification of the taxon validity.

Let's consider the case presented on Fig. 1A. One could define the taxon Polydactylia as follows: 'species that evolved from the evolving (segments of) metapopulation lineage in which the character state 'more than five digits on the limb', as exhibited by *gunnari* Jarvik, 1952 (assigned to the genus *Acanthostega* under Linnaean taxonomy) and *stensioei* Säve-Söderbergh, 1932 (assigned to the genus *Ichthyostega* under Linnaean taxonomy), has been acquired'.

The state 0 on Figs. 1A–C makes reference to the character state 'five or less digits on the limb', while 1 makes references to 'more than five digits on the limb'. Polydactylia belong to *Tetrapoda* as they exhibit four limbs. The author of this definition makes the hypothesis that exhibiting more than five digits on the limb is apomorphic with respect to the antonym of the character state, 'five or less digits on the limb'. This character is not applicable to the sister-group of *Tetrapoda*, as all lack limbs, hence neither adelphospecies nor amitaspecies of *Tetrapoda* can be identified regarding this character. Following the relationships presented on Fig. 1A, both adelphospecies and ami-

taspecies of Polydactylia can be identified and exhibit a character state different from the type character state of Polydactylia. Polydactylia is *Polydactylia*.

A subsequent phylogenetic analysis will likely demonstrate that the character state 'more than five digits on the limb' is a plesiomorphy at the level of *Tetrapoda* and a symplesiomorphy of cladotypic species (Figs. 1B,C). Based on the definition of homology proposed above, the character state is homologous in cladotypic species, but not derived. If *gunnari* and *stensioei* do not belong to a monophyletic clade but that including also those species exhibiting 'five or less digits on the limb' (Fig. 1B), there exists no sister-species of any lineage that gave rise to cladotypic species to exhibit a character state different from that exhibited by cladotypic species. In other words no adelphospecies of Polydactylia can be identified, hence neither is an amitaspecies. As formulated above, the polarity assumption allows the invalidation of the Polydactylia hypothesis. There is a case under which *gunnari* and *stensioei* belong to a monophyletic clade (Fig. 1C), and this clade has an adelphospecies (from which derived those species exhibiting 'five or less digits on the limb'). Therefore the amitaspecies of Polydactylia can be identified. It exhibits a character state identical to the lineage from which evolved cladotypic species. Therefore, based on the polarity assumption I propose, Polydactylia can be invalidated.

Now let's consider the case where a taxon is defined on a presumed reversion (Fig. 1D). One could define the taxon Apterygota as follows: 'species that evolved from the evolving (segments of) metapopulation lineage in which the character state 'lateral edges of thoracic terga rounded', as exhibited by *corticalis* Nicolet, 1842 (assigned to the genus *Entomobrya* under Linnaean taxonomy; springtail) and *saccharina* Linnaeus, 1758 (assigned to the genus *Lepisma* under Linnaean taxonomy; silverfish), has been acquired'. One of the antonyms of the defining character state is 'lateral edges of thoracic terga elongated', which could be seen as synonym of 'wings present', assuming that wings evolved from terga (which is followed for the sake of discussion). It must be noticed here that a formulation of Apterygota based on an alternative character state formulation could have been 'species that evolved from the evolving (segments of) metapopulation lineage in which the character state 'wings absent', as exhibited by *corticalis*, Nicolet, 1842 (assigned to the genus *Entomobrya* under Linnaean taxonomy; springtail) and *saccharina* Linnaeus, 1758 (assigned to the genus *Lepisma* under Linnaean taxonomy; silverfish), has been acquired'.

Following the frame proposed by SERENO (2007), the former definition involves a transformational character, while the latter involves a neomorphic character. It is my opinion that recourse to neomorphic formula-

tion is an outcome of incomplete knowledge on the origin of a structure, and should be avoided because the falsification of a taxon definition involving a neo-morphic character will be problematic, as non-existent attributes cannot be said to be homologous or non-homologous (RICHTER 2005). The example that follows makes reference to the former definition only, though 'elongated parts of thoracic terga' will be referred to as 'wings' from place to place for clarity (and above). The state 0 on Fig. 1D-J makes reference to the character state 'lateral edges of thoracic terga rounded' (i.e. 'wings absent'), while 1 makes references to 'lateral edges of thoracic terga elongated' (i.e. 'wings present').

A phylogenetic analysis could suggest that clado-typic species of Apterygota evolved from a unique lineage in which wings have actually been lost, hence exhibit 'lateral edges of thoracic terga rounded' (i.e. *Apterygota* would belong to *Pterygota*). If so, the amitaspecies of Apterygota would necessarily exhibit wings (Fig. 1D). The name Apterygota as defined above would then refer to a valid taxon. If it is subsequently proven that *corticalis* and *saccharina* lost wings independently (Fig. 1E), the homology assumption is not respected, and the taxon is invalid. The independent loss of wings is evidenced by the existence of distinct adelphospecies and amitaspecies for each cladotypic species. If *corticalis* happens to be nested within Pterygota but not *saccharina*, or if *saccharina* happens to be nested within Pterygota but not *corticalis* (Fig. 1F), the defining character state is not homologous among cladotypic species: several lineages from which directly evolved one of the cladotypic species exhibit another character state. Hence the name Apterygota does not refer to a valid taxon. Again, cladotypic species do not share a common amitaspecies. If both *corticalis* and *saccharina* happen to be nested outside of Pterygota (Fig. 1G,H), the rounded shape of the tergum (or lack of wings) is homologous in these species, but the defining character state is a symplesiomorphy of *corticalis* and *saccharina*. If *corticalis* and *saccharina* are found to belong to a monophyletic clade sister-group to *Pterygota* (Fig. 1G), the amitaspecies share the same character state as cladotypic species. If cladotypic species do not belong to a monophyletic clade, and if one of them belong to a lineage that is sister-group of the lineage in which wings have been acquired (Fig. 1H), one of the cladotypic species has no identifiable adelphospecies (and amitaspecies), while the amitaspecies of the other cladotypic species exhibits the defining character state of Apterygota. Therefore, the polarity assumption is not respected, and Apterygota can be invalidated. It is worth noting that if *corticalis* and *saccharina* are found to belong to a monophyletic clade by the virtue of another character state (Fig. 1G), the taxon Apterygota cannot be used

to name the corresponding clade (BÉTHOUX 2007a). One of the character states supporting the node must be used for a new definition, and an alternative name must be provided.

Ambiguity in the polarity of the type character state arises if the sister-species of the taxon [amitaspecies (adelphospecies, taxon T)] does exhibit the same character state as T, while the amitaspecies and the adelphospecies share the same character state different from that exhibited by T (Fig. 1F,G). Ambiguity arises also if the adelphospecies exhibit a character state different from a taxon T, while the character is not applicable in the amitaspecies. I follow the suggestion that a taxon is considered as valid until an unambiguous evidence of homoplastic distribution of the defining character state involving cladotypic species is provided (BÉTHOUX 2007a). In the case illustrated on Fig. 1F,G the taxon Apterygota keeps being valid.

Once it is accepted that polarity of the type character state constitutes a necessary assumption allowing a test of the validity of a taxon definition, it is then worth determining how this conceptual frame is distinct from the apomorphy-based definition as outlined in the PhyloCode (CANTINO & DE QUEIROZ 2006). Unlike I mentioned earlier (BÉTHOUX 2007a), an apomorphy-based definition does not necessarily define a monophyletic taxon. One could define Apterygota as species sharing the character (state) 'lateral edges of thoracic terga rounded', as in *Lepisma saccharina*. This definition could be based on the assumption that winglessness is an apomorphy of silverfishes and of some unspecified related species, based on a phylogenetic analysis nesting silverfishes within Pterygota. The taxon could be designated as being 'apophyletic' (defined on the basis of an apomorphy). If a subsequent phylogenetic analysis likely demonstrates that the character state is a symplesiomorphy of Apterygota and Pterygota, the character state 'lateral edges of thoracic terga rounded' is not apomorphic of any taxon. The defined taxon could be said to be monophyletic by the virtue of referring to a single species, but this makes little sense. Because composition is an outcome of definitions under the PhyloCode (as well as under cladotypic taxonomy), this taxon is neither paraphyletic nor polyphyletic. I am not aware of any word allowing the status of a taxon defined in such a way, thus I propose to introduce the word 'plesio-phyletic' (i.e. defined on the basis of a plesiomorphy).

Under the cladotypic system as implemented herein, the falsification process faces several possible cases (Fig. 1). A taxon can be valid (Fig. 1A,D,I,J) and designated as 'synapophyletic' (defined on the basis of a synapomorphy). In the case presented on Fig. 1E, the first assumption is not respected, and Apterygota is a 'diapophyletic' assemblage of species (defined on the basis of a convergence). In the case presented on

Fig. 1F, the defining character state is not homologous among cladotypic species, hence the first assumption is not respected. In such a case the assemblage is not strictly speaking diapophyletic. I propose the word 'asymphyletic' (from 'asymphylos', 'not of the same race' in Greek) for such assemblages of species. If both *corticalis* and *saccharina* happen to be nested outside of *Pterygota* (Fig. 1G,H), the lack of wings is homologous in these species (i.e., the first assumption is valid), but the polarity assumption is erroneous. Even if *corticalis* and *saccharina* are found to belong to a monophyletic clade (Fig. 1G), Apterygota is an invalid hypothesis and this assemblage of species can be designated as being 'symplesiophyletic' (defined on the basis of a symplesiomorphy; see also Fig. 1B,C).

In summary, synapophyletic, diapophyletic, asymphyletic, and symplesiophyletic assemblages of species can be named under cladotypic taxonomy. Under apomorphy-based definitions only apophyletic and plesiophyletic assemblages can be named. This is related to the mandatory use of two cladotypes, itself related to the first assumption. This difference is related to the reliance on different sets of assumptions. It must be reminded that the mandatory recourse to three specifiers as under cladotypic taxonomy allows problems of apomorphy-based definitions as listed by Sereno (1999) to be solved (Béthoux 2007a). The cladotypic system appears as distinct from the apomorphy-based one, though they share analogies.

5. Practical version of the second assumption

The problem with the isolation assumption (*cohesion mechanisms isolated individuals exhibiting the type character state from those that do not*) is that it applies only if the acquisition of the defining character-state *resulted* into cohesion mechanisms *responsible* for the isolation of the corresponding taxon. I (Béthoux 2007a: 414) mentioned that "In practice, the type character state will likely be a trait fixed later than the isolation event, in one of the successive anagenetic infra-specific entities that cumulated traits, in relation to the various processes responsible for the existence of species". If so, the second assumption does not apply: individuals exhibiting the type character state belong to the same evolving (segments of) metapopulation lineages as those that do not share it. If it cannot be proven that the defining character-state resulted into cohesion mechanisms responsible for the isolation of the corresponding lineage, I propose an isolation assumption alternative to the original one, as follows: *individuals exhibiting the type character state evolved*

from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms.

6. Conclusion

The hypothesis on the derivation of a group of species from a unique ancestral species is primarily based on a character state shared by these species. As implemented herein, each hypothesis of unique ancestry (i.e. a taxon hypothesis) is based on three falsifiable assumptions. First, it is assumed that the character state is homologous among cladotypic species (*the character state typified by cladotypes is homologous in individuals that are designated as cladotypes*; homology assumption). Second, it is assumed that the character state is derived (*an amitaspecies can be identified and, regarding the character involved in the definition, it exhibits a character state different from that exhibited by the taxon*; polarity assumption). Third, it is assumed that the character state, arguably homologous and derived, has been acquired in a lineage isolated from other lineages (*cohesion mechanisms isolated individuals exhibiting the type character state from those that do not*, or *individuals exhibiting the type character state evolved from a (segments of) metapopulation lineage isolated from other such lineages by cohesion mechanisms*; isolation assumption). Coupled with the explicit reference to homology and character state polarity, cladotypic taxonomy could ultimately be viewed as (a) cladistic taxonomy, though 'taxon' is considered as a subset of the 'species' category.

7. Acknowledgments

8. References

Béthoux, O. 2007a. Propositions for a character-state-based biological taxonomy. – Zoologica Scripta **36**: 409–416.

Béthoux, O. 2007b. Cladotypic taxonomy applied: titanopterans are orthopterans. – Arthropod Systematics & Phylogeny **65**(2): 135–156.

Cantino, P.D. & de Queiroz, K. 2006. International code of phylogenetic nomenclature. Version 3a. Part 1: Clade names 2006 [Available from http://www.ohiou.edu/phylocode/]

DARWIN, C. 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. I. Extract from an unpublished work on species, II. Abstract of a letter from C. Darwin, Esq., to Prof. Asa Gray. – Journal of the Proceedings of the Linnaean Society of London **3**: 45–53.

DARWIN, C. 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. – John Murray, London. 32 pp.

DAYRAT, B., SCHANDER, C. & ANGIELCZYK, K. 2004. Suggestions for a new species nomenclature. – Taxon **53**: 485–491.

DE PINNA, M.C.C. 1991. Concepts and tests of homology in the cladistic paradigm. – Cladistics **7**: 367–394.

DE QUEIROZ, K. 2005a. Ernst Mayr and the modern concept of species. – Proceedings of the National Academy of Sciences of the United States of America 102: 6600–6607.

DE QUEIROZ, K. 2005b. Different species problems and their resolution. – Bioessays **27**: 1263–1269.

HENNIG, W. 1966. Phylogenetic Systematics. – University of Illinois Press, Urbana. 263 pp.

JARVIK, E. 1952. On the fish-like tail in the ichtyostegid stegocephalians. – Meddelelser om Grønland **114**: 1–90.

LINNAEUS, C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus differentiis, synonymis, locis. – Stockholm. 824 pp.

NICOLET, H. 1842. Recherches pour servir à l'histoire des podurelles. – Nouveaux Mémoires de la Société Helvétique des Sciences Naturelles **6**: 1–88.

RICHTER, S. 2005. Homologies in phylogenetic analyses – concept and tests. – Theory in Biosciences **124**: 105–120.

SÄVE-SÖDERBERGH, G. 1932. Preliminary note on Devonian stegocephalians from East Greenland. – Meddelelser om Grønland **98**: 1–211.

SERENO, P.C. 1999. Definitions in phylogenetic taxonomy: critique and rationale. – Systematic Biology **48**: 329–351.

SERENO, P.C. 2007. Logical basis for morphological characters in phylogenetics. – Cladistics; **23**: 1–23.

WALLACE, A.R. 1858. On the tendency of species to form varietes; and on the perpetuation of varieties and species by natural means of selection. III. On the tendency of varieties to depart indefinitely from the original type. – Journal of the Procee dings of the Linnaean Society of London **3**: 53–62.