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ORIGINAL ARTICLE

The criterion of conjunction in plant systematics and evolution

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Abstract

I review the theory and practice behind as reported by Patterson (in: Joysey, Friday (eds) Problems of phylogenetic reconstruction, Academic Press, London, 1982) the criterion of conjunction in plant systematics and evolution, with a focus on: (1) de Pinna (Cladistics 7:367–394, 1991) analysis of homology in the cladistic framework; (2) Hawkins' (in: Scotland, Pennington (eds) Homology and systematics: coding characters for phylogenetic analysis, Taylor and Francis, London, 2000) survey of character coding; (3) Sereno (Cladistics 23:565–587, 2007) view of neomorphic and transformational characters; (4) character coding and polymorphic taxa; and (5) the relationship between character coding and plant variation using examples cited by Hawkins (in: Scotland, Pennington (eds) Homology and systematics: coding characters for phylogenetic analysis, Taylor and Francis, London, 2000). I coin the term "Replicable homology," in contrast to serial homology, to make reference to the presence of multiple copies of the same structure or part in the same organism. I conclude that by Patterson's (in: Joysey, Friday (eds) Problems of phylogenetic reconstruction, Academic Press, London, 1982) criterion is an important tool in order to identify neomorphic characters and that it cannot be applied to transformational characters. Conventional coding is the appropriate way to code characters, whereas both conjunction and unifying coding should be abolished from character analysis, as they are in disagreement with the view that a single character state must contain a mutually exclusive condition in relation to other character states.

Keywords Character · Character coding · Character states · Homology · Neomorphic characters · Transformational characters

Introduction

In his influential chapter entitled *Morphological characters and homology*, Patterson (1982) commented on three integrated ways to access homology (i.e., the same feature shared by two or more species through a common evolutionary history) in cladistics: (1) similarity; (2) congruence; and (3) conjunction. Among these tests, the most discussed have been similarity and congruence (e.g., de Rieppel 1988; de Pinna's (1991); Franz 2005; Rieppel and Kearney 2002; Kearney and Rieppel 2006; Assis 2009). *Similarity "may be of any kind (topographic, ontogenetic, histological,* etc.*)* […]" (Patterson (1982, p. 8). It means that a structure or part in two or more organisms represents the same character on the basis of its position, ontogeny, and genetics. *Congruence means that "synapomorphies are the only properties of monophyletic groups, tests of a hypothesis of homology must be other hypotheses of homology—other synapomorphies*" (Patterson (1982, p. 38). It implies that this same structure or part originated only once, i.e., it is either a synapomorphy or metapomorphy (Assis 2017), within a particular phylogenetic scenario. Yet, if this same part originated multiple times, it is a homoplasy (Scotland 2011; Assis 2017). *Conjunction implies that "If two structures are supposed to be homologous, that hypothesis can be conclusively refuted by finding both structures in one organism*" (Patterson (1982, p. 38) (Table 1). Conjunction, however, has received a few comments (de Pinna 1991; Hawkins 2000; Williams and Ebach 2008).

In this article, I review the theory and practice behind the criterion of conjunction in plant systematics and evolution, with a focus on: (1) de Pinna's (1991) analysis of homology in the cladistic framework; (2) Hawkins (2000) survey of

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Table 1 Integrated ways of delimiting homology (Patterson 1982) and their relationships with neomorphic and transformational characters (Sereno 2007)

Ways of homology delimitation	Neomorphic characters	Transformational characters	Impact in phylogenetic reconstruction
Similarity	Yes	Yes	It implies that two or more structures and their variables found in two or more organism are the same
Conjunction	Yes	No	It implies that two structures found in the same organism are not the same
Congruence	Yes	Yes	It implies that a structure and its variables found in two or more organisms originated once (homology) or more times (homoplasy) in the phylogeny

character coding; (3) Sereno's (2007) view of neomorphic and transformational characters; (4) character coding and polymorphic taxa; and (5) the relationship between character coding and plant variation using examples cited by Hawkins (2000).

The criterion of conjunction after Patterson

After Patterson (1982), few authors (de Pinna 1991; Hawkins 2000; Williams and Ebach 2008) discussed the conjunction criterion. According to de Pinna (1991, p. 367; see also Williams and Ebach 2008):

> "Of three tests of homology proposed to date (similarity, conjunction and congruence) only congruence serves as a test in the strict sense. Similarity stands at a basic level in homology propositions, being the source of the homology conjecture in the first place. Conjunction is unquestionably an indicator of non-homology, but it is not specific about the pairwise comparison where non-homology is present, and depends on a specific scheme of relationship in order to refute a hypothesis of homology. The congruence test has been previously seen as an application of compatibility analysis. However, congruence is more appropriately seen as an expression of strict parsimony analysis."

In this way, de Pinna (1991) reinforced, like Patterson (1982), the importance of the conjunction criterion to identify that two structures are not homologous.

Hawkins (2000, p. 32) discussed the criterion of conjunction with respect to character codification, specifically the "conjunction coding":

> "Although seemingly very simple, the conjunction argument is a difficult one because conjunction can be interpreted in two ways. Firstly, the conjunction argument may be used to dictate the form of primary homology statement, like the similarity criterion operating logically prior to the congruence test. In this case the coding 'tail colour: red (0) blue (1) red and blue (2)' should not be employed when redness and blueness co-occur in a single organism, since the criterion is failed. The occurrence of redness and blueness together informs us that the two are not homologous—thus they should not be encoded as putative homologues, i.e. as a single primary homology statement. An alternative coding should be used which does not include redness and blueness within a single character data matrix."

Hawkins (2000, p. 33) stressed that Patterson's (1982) criterion of conjunction is rare, citing Rudall and Cutler (1995, p. 160), who noted that both styloids and raphides may coexist in the same plant; therefore, they should be treated as independent characters. On the basis of Hawkins' (2000) analysis, it is important to differentiate the criterion (or argument) of conjunction from conjunction coding. The first relates to Patterson's (1982) criterion, whereas the latter relates to a kind of character codification, which "*recognises two character states, and includes a third character state to account for organisms which show both states"* (Hawkins 2000, p. 25). In addition, Hawkins (2000, p. 25) stated that "*conjunction coding differs from unifying coding which is concerned with conceptualizing characters where taxa may be polymorphic, whereas conjunction coding refers to 'polymorphism' within an individual organism.*" Finally, Hawkins (2000, p. 33) concluded that "*use of the 'conjunction coding' in the literature demonstrates the need for a re-evaluation of the role of the conjunction argument* [or criterion]." Yet, she stressed that "conjunction coding should be avoided because the independent states are coded as one character."

The criterion of conjunction and the view of neomorphic and transformational characters

According to Sereno (2007, p. 565), "*characters are simply features expressed as independent variables and character states the mutually exclusive conditions of a* *character*." In addition, he defined two kinds of character in phylogenetics, i.e., neomorphic and transformational:

> "Neomorphic characters are composed only of locators, and their character states are limited to 'present' and 'absent'. […] A new bone, such as the predentary of ornithischian dinosaurs, is a neomorphic character that lacks any comparable transformational state among outgroup taxa. The character simply identifies the bone. There is no hypothetical or proposed transformation between the predentary and another bone; the bone is either present or absent" (p. 573).

> "Transformational characters, unlike neomorphic characters, include a variable. Transformational character states are mutually exclusive conditions of that variable […]. Transformational characters, when completely formulated with an appropriate variable, 'imply their respective conditions' […]. The variable in a transformational character restricts the realm of possible character states" (p. 574).

These propositions of character are represented in Sereno's (2007) logical analysis of morphological characters as follows: Neomorphic characters are represented by a locator L (a term that points to a particular structure or part) and their states (i.e., conditions of either a structure or variable of a structure) $v_{0;1,}$; transformational characters by a locator L, a variable V (i.e., an aspect of the structure that variates), and their states $v_{0;1;2;...}$).

Returning to Patterson's definition (1982, p. 38): "*If two structures are supposed to be homologous, that hypothesis can be conclusively refuted by finding both structures in one organism.*" Here, it is critical to understand what Patterson (1982) wanted to say when he made reference to "*two structures*." In my understanding, Patterson's (1982) view of "structures" is equivalent to neomorphic characters, so that the conjunction criterion cannot be applied to transformational characters (Table 1). Indeed, if structures are understood as neomorphic characters, Patterson's criterion is successful, because two neomorphic characters cannot be homologous to each other. By contrast, Hawkins (2000) applied the criterion of conjunction to transformational characters, as seen in the example "tail colour: red (0) blue (1) red and blue (2)." However, following the arguments endorsed here, this example cannot be treated in the context of Patterson's (1982) criterion of conjunction. In line with this, if two or more states (i.e., conditions of the variable of a character sensu Sereno 2007) of a transformational character are found in the same organism, they cannot be delimited as distinct characters. However, the most important point is to know whether these character states make part of a single character or structure (sensu Patterson 1982).

Character coding and polymorphic taxa

With respect to polymorphic taxa, both conjunction and unifying coding create a single character state that embraces two or more conditions of the variable of a character, e.g., "tail colour: red (0) blue (1) red and blue (2)." The character state (2) does not represent an exclusive condition, as it embraces the conditions (0) and (1). By contrast, the conventional coding creates only two character states, e.g., "tail colour: red (0) blue (1)." Using both conjunction and unifying coding in a taxonomic data matrix, a polymorphic taxon would be marked with the character state (2). Using the conventional coding, it would be marked with both character states (0) and (1). Wiens (1999, pp. 332–333) called these two ways of coding "Scaled" and "Polymorphic," respectively. According to him, the "Scaled" codification provides phylogenetic information, as the character state (2) can be read as apomorphic information. By contrast, the "Polymorphic" codification is uninformative in the phylogenetic inference (Table 2).

A criticism to the "Scaled" codification is that the character state (2) is not really a new condition, but the sharing of the conditions (0) and (1). Consequently, it cannot be considered a genuine apomorphy sensu Hennig (1966). This criticism is in agreement with the view that a single character state must contain a mutually exclusive condition in relation to other character states (Sereno 2007). Consequently, both conjunction and unifying coding (and the Scaled codification) should be abolished from data matrices, and only the conventional coding (and Polymorphic codification) applied.

Hawkins' analysis of character coding and the plant variation

Hawkins (2000) commented on ten examples of conjunction coding found in the phylogenetic studies conducted by Cox et al. (1995), Goldblatt (1995), Linder and Kellogg (1995), Stevenson and Loconte (1995), Uhl et al. (1995), and Hufford (1996). Although she stressed that the conjunction coding should be abolished from character coding, and that only the conventional coding should be used, she did not re-codify the characters proposed by those authors. In this section, following Sereno's (2007) logical analysis, I further revise these characters, discuss whether Patterson's (1982)

Table 2 Kinds of character coding in polymorphic and non-polymorphic taxa

Kinds of coding	Polymorphic taxa Character: character states	Non-polymorphic taxa Character: character states	Impact in phylogenetic reconstruction including polymorphic taxa
Conventional	Tail color: red (0) blue (1)[a]	Tail color: red (0) blue (1)	Phylogenetically uninformative and in agreement with the view that a single character state must contain a mutually exclusive condition in relation to other character states
Conjunction	Tail color: red (0) blue (1) red and blue (2)[b]	–	Phylogenetically informative and in disagreement with the view that a single character state must contain a mutually exclusive condition in relation to other character states
Unifying	Tail color: red (0) blue (1) red and blue (2)[c]	–	Phylogenetically informative and in disagreement with the view that a single character state must contain a mutually exclusive condition in relation to other character states

[a] Polymorphic coding (Wiens 1999)

[b, c] Scale coding (Wiens 1999)

criterion of conjunction should be applied to them, and make new propositions of character coding.

Cox et al. (1995)

Character 13. Root vessels with both scalariform and simple perforation plates: no (0) yes (1).

Comment. Cox et al. (1995), instead of treating scalariform and simple perforations as distinct character states, constructed a character embracing these two kinds of perforation, with two states "no (0) yes (1)." Although this treatment is different from the classical example of conjunction codification presented by Hawkins (2000, p. 25), Cox et al. (1995) observed that both kinds of perforation co-occur in the same organism. In fact, these two kinds of perforation represent a transformational character. Consequently, it does not make sense to use Patterson's (1982) criterion of conjunction to say that "scalariform" and "simple" plates are not the same structures. A proposition of conventional coding is here used, instead of using the conjunction coding as done by Cox et al. (1995).

New character coding proposition. Root, vessels, perforation: scalariform (0) simple (1). Transformational character (L_1, L_2, V: v_0; v_1).

Goldblatt (1995)

Character 5. Calcium oxalate present: as raphides (0) cuboidal crystals (1) raphides and styloids (2) styloids (3) crystal sand (4) none (5).

Comment. A way to deal with this example would be to treat raphides and styloids as distinct characters, i.e., they are not the same structures (e.g., Rudall and Cutler 1995). However, if oxalate calcium is the same element with different shapes, these same shapes represent states of a transformational character. In line with this, I figure out that Rudall and Cutler (1995) applied equivocally Patterson's (1982) criterion of conjunction to the variable (i.e., form) of a transformational character, thus decomposing this character into two neomorphic characters. The character proposed by Goldblatt (1995) is decomposed here into two characters, i.e., neomorphic and transformational, and the conventional coding is adopted.

New character coding propositions. Calcium oxalate: absent (0) present (1). Neomorphic character (L_1: v_0; v_1). Calcium oxalate, form: raphides (0) cuboidal crystals (1) styloids (2) crystal sand (3). Transformational character (L_1, V: v_0; v_1; v_2).

Character 21. Perianth whorls: both calycine (0) petaloid (1) outer calycine, inner petaloid (2).

Comment. The two whorls of perianth represent a case of serial homology or homonomy (cf. Patterson 1988; Wagner 2014). In this case, both whorls constitute independent characters. Serial homology, therefore, helps us to understand this character analysis. Patterson's criterion (1982) is applicable here, because each whorl of perianth is a neomorphic character. Hence, it would not be adequate to apply the conjunction coding, as made by Goldblatt (1995). The single character proposed by Goldblatt (1995) is decomposed here into four characters: two neomorphic and two transformational. The conventional coding is also applied here.

New character coding propositions. Perianth, outer whorl: absent (0) present (1). Neomorphic character (L_1, L_2: v_0; v_1). Perianth, outer whorl, form: calycine (0) petaloid (1). Transformational character (L_1, L_2, V: v_0; v_1). Perianth, inner whorl: absent (0) present (1). Neomorphic character (L_1, L_2: v_0; v_1). Perianth, inner whorl, form: calycine (0) petaloid (1). Transformational character (L_1, L_2, V: v_0; v_1).

Character 23. Stamens: six in two whorls (0) inner whorl lacking (1) at least posterior three stamens lacking (2).

Comment. With at least posterior three stamens lacking one refers to a totally different set of characters such as monosymmetry which can be related to stamen loss. The two whorls of stamens represent a case of serial homology or homonomy (cf. Patterson 1988; Wagner 2014). In this case, both whorls constitute independent characters. Serial homology, therefore, helps us to understand this character analysis. Patterson's criterion (1982) is also applicable here, so that it would not be adequate to apply the conjunction coding, as made by Goldblatt (1995). The single character proposed by Goldblatt (1995) is decomposed here into two neomorphic characters. Conventional coding is also applied here.

New character coding propositions. Stamens, outer whorl: absent (0) present (1). Neomorphic character (L_1, L_2: v_0; v_1). Stamens, inner whorl: absent (0) present (1). Neomorphic character (L_1, L_2: v_0; v_1).

Linder and Kellogg (1995)

Character 8. Sieve tube plastids: with protein bodies and starch grains (0) with only protein bodies (1) with only protein bodies, but these with fragments (2).

Comment. A way to deal with this example would be to treat protein bodies and starch grains as distinct characters, because they are not the same structures. Although both conditions occur in the same structure, protein bodies cannot be transformed into starch grains, neither the other way around. In other words, there is not a relation of transformational homology (cf. Rieppel 1988; Brower 2015) between these conditions. In this case, Patterson's (1982) criterion helps us, so that both character states should be treated as distinct neomorphic characters. In turn, the character proposed by Linder and Kellogg (1995) is decomposed here into two neomorphic characters.

New character coding propositions. Sieve tube, plastids, protein bodies: absent (0) present (1). Neomorphic character (L_1, L_2, L_3: v_0; v_1). Sieve tube, plastids, starch grains: absent (0) present (1). Neomorphic character (L_1, L_2, L_3: v_0; v_1).

Stevenson and Loconte (1995)

Character 4. Lateral root origination: opposite xylem (0) opposite phloem (1) both (2).

Comment. Lateral roots are considered homologous within monocotyledons. Thus, both states cannot be considered distinct neomorphic characters, but states of a transformational character. Here, the use of Patterson's (1982) criterion is not applicable. Differently from Stevenson and Loconte (1995), who used conjunction coding, a conventional coding is proposed here.

New character coding proposition. Root, lateral, origination: opposite xylem (0) opposite phloem (1). Transformational character (L_1, L_2, V: v_0; v_1).

Character 39. Number of stamens: one (0) two (1) three from both whorls (2) four (3) five (4) six (5) many (6) three from inner whorl (7) three from outer whorl (8).

Comment. The two whorls of stamens represent a case of serial homology or homonomy (cf. Patterson 1988; Wagner 2014). In this case, both whorls constitute independent characters. Serial homology, therefore, helps us to understand this character analysis. Patterson's (1982) criterion is applicable here. Hence, it would not be adequate to apply the conjunction coding, as made by Stevenson and Loconte (1995). An unsolved issue here is when a taxon has a single whorl. Is it either the outer or inner whorl? The single character proposed by Stevenson and Loconte (1995) is decomposed here into four characters: two neomorphic and two transformational. The conventional coding is also applied here.

New character coding propositions. Stamens, outer whorl: absent (0) present (1). Neomorphic character (L_1, L_2: v_0; v_1). Stamens, outer whorl, number: one (0) two (1) three (2) four (3) five (4) six (5) many (6). Transformational character (L_1, L_2, V: v_0; v_1; v_2; $v_{3;}$ v_4; v_5). Stamens, inner whorl: absent (0) present (1). Neomorphic character (L_1, L_2: v_0; v_1). Stamens, inner whorl, number: one (0) two (1) three (2). Transformational character (L_1, L_2, V: v_0; v_1; v_2; $v_{3;}$ v_4; v_5).

Uhl et al. (1995)

Character 19. Flowers: bisexual only present (0) bisexual and unisexual present (1) unisexual only (2).

Comment. Bisexual and unisexual flowers co-occurring in the same organism does not imply that these flowers are not composed by the same parts. Plants have multiple meristems from which the *same* structures or parts may develop multiple times. Serial homology implies the origin of *similar* structures, but not the *same* structures (Wagner 2014). By contrast, I will call "Replicable homology" the presence of multiple copies of the *same* structure or part in the *same* organism. In line with this, flowers with the same parts in the same organism illustrate a case of replicable homology, whereas stamens in a single flower illustrate a case of serial homology. Thus, replicable homology and serial homology represent different patterns of morphological variation within a single organism. Once bisexual and unisexual flowers are states of a transformational character, the use of Patterson's (1982) criterion is not applicable here. Differently from Uhl et al. (1995), who used conjunction coding, a conventional coding is proposed here.

New character coding proposition. Flowers, sexuality: bisexual (0) unisexual (1). Transformational character (L_1, V: v_0; v_1).

Hufford (1996)

Character 4. Female inflorescences: racemes or axillary flowers (0) strictly axillary flowers (1).

Comment. I interpret raceme and axillary flowers as two patterns of floral phyllotaxy: The first is alternate and the latter is verticillate. Axillary flowers imply that the flowers originate from a single node. Instead of indicating the types of inflorescence, as made by Hufford (1996), the new proposition provided here takes into account the patterns of phyllotaxy. As this is a transformational character, Patterson's (1982) criterion is not also applicable here.

New character coding proposition. Inflorescence, flowers, phyllotaxy: alternate (1) verticillate (1). Transformational character (L_1, V: v_0; v_1).

Conclusions

Regarding the importance of the analysis of morphological characters in systematics and evolution (Scotland and Pennington 2000), a review of Patterson's (1982) criterion of conjunction is constructive. In contrast to Hawkins' (2000) view, there is not a problem with his criterion, but there is a problem with her interpretation. In Patterson's (1982, p. 38) view, the term "structures" is equivalent to neomorphic characters, not to states of the variable of a transformational character. Therefore, Patterson's criterion is an important tool in order to identify neomorphic characters. Accordingly, if two or more character states of a transformational character are found in the same organism, this does not imply that these states should be codified as distinct characters. Regarding the view of character states as mutually exclusive conditions of a character, conventional coding is the most appropriate way to coding characters, whereas both conjunction coding and unifying coding should be abolished from character coding.

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Conflict of interest I declare that there is no conflict of interest relative to the article.

Human and animal rights This work did not involve animal and human participants as subjects.

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