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Ensayo

# CLADISTIC METHODS TO ANALYZE ADAPTATION

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**RESUMEN.** Los cladogramas obtenidos independientemente de teorías sobre procesos evolutivos, como por ejemplo adaptación, pueden ser usados para contrastar dichas teorías. En este trabajo revisamos brevemente los pasos seguidos en el enfoque cladístico del estudio de la adaptación, como el mapeo de caracteres y la optimización de caracteres binarios y multiestados, y comparaciones entre grupos hermanos. Se presentan dos estudios de caso para ejemplificar este enfoque, uno referido a acridios (Orthoptera: Acrididae) y el otro a gorgojos (Coleoptera: Curculionoidea).

PALABRAS CLAVE: Adaptación, cladística, Orthoptera, Acrididae, Coleoptera, Curculionoidea.

**ABSTRACT.** Cladograms obtained independently of theories about evolutionary processes, e.g., adaptation, can be used to test such theories. In this paper, we briefly review the steps to be followed in a cladistic approach to the study of adaptation, namely, character mapping and optimisation of binary and multistate characters, and sister group comparisons. Two case studies are presented to exemplify this approach, one dealing with grasshoppers (Orthoptera: Acrididae) and the other with weevils (Coleoptera: Curculionoidea).

KEY WORDS: Adaptation, cladistics, Orthoptera, Acrididae, Coleoptera, Curculionoidea.

The search for a functional or adaptive fit between an organism and its environment is one of the dominant themes in evolutionary biology. Brooks & McLennan (1991) consider that adaptation has three components: origin, diversification, and maintenance of characters. Microevolutionary studies at the population level concentrate on the maintenance of traits in current environments, where processes shaping the interactions between the organism and its environment can be observed and measured directly (Maynard-Smith, 1978; Oster and Wilson, 1978). The study of the two other components of adaptation, the origin and diversification of characters, is undertaken by the macroevolutionary approaches. The importance of adaptation as a key factor to explain diversification at higher taxonomic levels, however, remained quite speculative until recently, when some authors developed cladistic tests of adaptational hypotheses (Coddington, 1988, 1990; Carpenter, 1989; Lauder 1990; Baum & Larson, 1991; Brooks & McLennan, 1991; Grandcolas *et al.*,1994, 1997).

The use of tests of evolutionary scenarios by reference to phylogenetic hypotheses is increasingly recognised as a pertinent approach in comparative studies (Coddington 1988; Wanntorp *et al.*, 1990; Baum & Larson, 1991; Armbuster, 1992; Miles & Dunham, 1993; Wenzel & Carpenter, 1994; Grandcolas *et al.*, 1994; Andersen, 1995; Losos, 1996; Ornelas, 1998). The development of cladograms independently of theories about evolutionary processes makes tests of such theories possible. Patterns predicted from process theories may be thus contrasted with the general patterns predicted by the cladograms, which summarise the genealogical evidence (Carpenter, 1989).

In this paper we briefly review the general steps to be followed in studies of adaptation related to the origin and diversification of characters in a cladistic framework, and examine two case studies dealing with grasshoppers (Orthoptera: Acrididae) and weevils (Coleoptera: Curculionoidea).

## ORIGIN OF ADAPTIVE CHARACTERS

Baum & Larson (1991) described a general protocol for discerning adaptations, that synthesised and refined a phylogenetically based definition of adaptation. This protocol has eight steps:

(1) Choice of subject taxa.
(2) Phylogeny reconstruction.
(3) Scoring characters.
(4) Scoring selective regime.
(5) Partitioning character change on the phylogeny.
(6) Inferring selective regimes of ancestral lineages.
(7) Assessing current utility.
(8) Classifying traits into categories of utility/historical genesis.

In their description, and following Gould & Vrba (1982), an adaptation is a character that must have current utility, i.e., exhibits a performance advantage, and was generated historically through action of natural selection for its current biological role. Baum & Larson's (1991) approach to adaptation may be summarised as follows:

(1) Identification of those lineages in which a trait transformation is evident. This is necessary for the comparison of the historical antecedent state (plesiomorphic vs. apomorphic state).

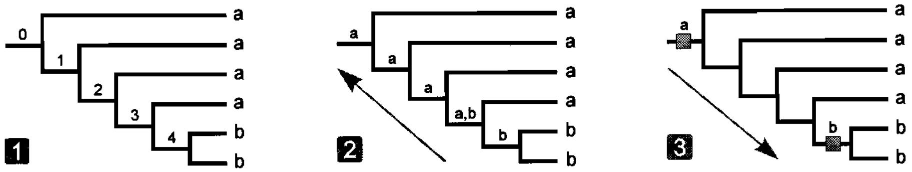
(2) Mapping of functional capacity on the phylogenetic hypothesis to determine the transformation sequence for performance.

(3) Determination of the shift in the environment with respect to the genealogical relationships of the taxa as portrayed in the cladogram. The hypothesised

environmental change may be related to alterations in the "selective regime" experienced by the taxa.

The aim of this protocol is to identify the occurrence of a shift in the selective regime, where the selective regime changed in the phylogeny, and whether it is concordant with the transformation of the trait and its function. Adaptations may thus be autapomorphic (unique to a single taxon), synapomorphic (unique to a single clade), or occur independently (homoplasious), but must show a concordant shift in their performance.

Character mapping and optimisation represents the simplest method that can be used to test the origin of adaptive characters in a cladistic framework (Miles & Dunham, 1993). It consists basically in mapping the independent origins of a trait onto a cladogram and optimising its ancestral character states, mostly using Farris's (1970) optimisation procedure (Carpenter, 1989; Mickevich & Weller, 1990; Brooks & McLennan, 1991). Optimisation implies that the number of steps involved in the character transformation is minimised (Donoghue, 1989; Hills & Green, 1990; Wenzel & Carpenter, 1994). We will examine this procedure with different hypothetical examples (Figs. 1-10):



Figs. 1-3. Optimisation of a binary character. Explanation in text.

**Binary character** (Figs. 1-3). The cladogram of figure 1 shows the distribution of a binary character with states 'a' and 'b' mapped at the terminal taxa. Optimisation of this character requires two steps:

(1) "Generalising down" the cladogram (Fig. 2). Label the nodes, beginning with the node corresponding to the least inclusive group, by considering the intersection of the character states of the two closest nodes or branches, in the following manner:

(a) if the two closest nodes or branches are either both 'a', or 'a' and 'a and b', label the node 'a';

(b) if the two closest nodes or branches are either both 'b', or 'b' and 'a and b', label the node 'b';

(c) if the two closest nodes or branches have different labels (one 'a' and the other 'b'), label the node 'a, b';

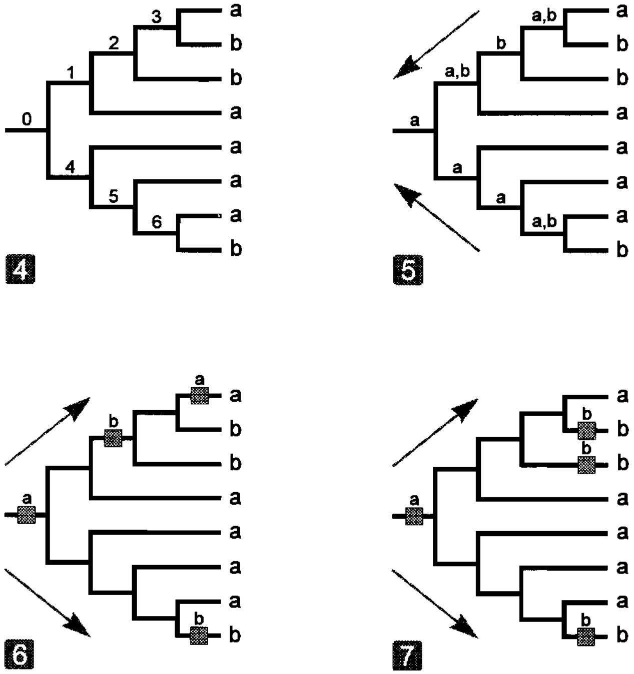
(d) continue with this procedure toward the root of the cladogram.

(2) "Predicting up" the cladogram (Fig. 3). Move from the root up the cladogram, resolving ambiguities by comparing the ambiguous node with the value of the node directly below it. In the example, only node number 3 is ambiguous, and because the value of the node below it (number 2) is 'a', it is reassigned state 'a'.

Now that all nodal states have been resolved in the cladogram, the character is hypothesised to have the ancestral condition 'a', which changed to 'b' in the ancestor of the two species that now exhibit state 'b'.

The cladogram of figure 4 shows a more complex example of the distribution of a binary character. The two same steps are followed:

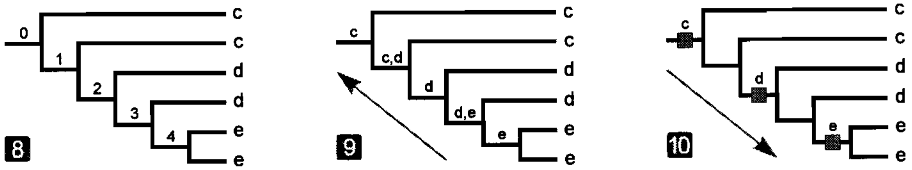
(1) "Generalising down" the cladogram (Fig. 5). Label the nodes, beginning with the node corresponding to the least inclusive group, following the same logic that in the first example. According to this cladogram, nodes 0, 4, and 5 are labelled with state 'a', node 2 is labelled 'b', and nodes 1, 3, and 6 are considered ambiguous ('a, b').



Figs. 4-7. Optimisation of an ambiguous binary character. Explanation in text.

(2) "Predicting up" the cladogram (Fig. 6). When proceeding with this step, the solution of figure 6 indicates that 'a' is plesiomorphic, it evolves to 'b' in nodes 2 and 6, reversing once to 'a'. This implies that not all species bearing character state 'a' inherited it from the same ancestor.

The relative amount of parallelisms and reversals can be used to choose among competing equally parsimonious cladograms. When reversals are preferred over parallelisms, character state changes are placed closer to the root of the cladogram, and homoplasy tend to be explained in terms of more distal reversals (Fig. 6), which is called "accelerated character transformation" (ACCTRAN; Swofford & Maddison, 1987). On the contrary, if reversals are *a priori* minimised, the proportion of homoplasy that is caused by parallelisms is maximised (Fig. 7), which is called "delayed character transformation" (DELTRAN; Swofford & Maddison, 1987).



Figs. 8-10. Optimisation of a multistate character. Explanation in text.

**Multistate character** (Figs. 8-10). The cladogram of figure 8 shows the distribution of a multistate character with states 'c', 'd', and 'e' mapped at the terminal taxa. Optimisation of this character requires the same steps:

(1) "Generalising down" the cladogram (Fig. 9). Label the nodes, beginning with the node corresponding to the least inclusive group, following the same logic that in the first example. In this way, node 0 is labelled with state 'c', node 1 is ambiguous ('c, d'), node 2 is labelled 'd', node 3 is ambiguous ('d, e'), and node 4 is labelled 'e'.

(2) "Predicting up" the cladogram (Fig. 10). Move from the root up the cladogram, resolving ambiguities as in the previous example. Node 1 is reassigned a value of 'c' and node 3 is labelled 'd'.

Now that nodal states have been resolved in the cladogram, the character is hypothesised to have the ancestral condition 'c', which changed to 'd' in ancestor 2, and then further changed to 'e' in ancestor 4.

**Case study.** Cigliano *et al.* (1996) conducted a phylogenetic analysis of the South American grasshopper genus *Scotussa* and its closest relatives (Orthoptera: Acrididae). The cladogram obtained can be used to test the association between the structural change in the ovipositor valves and the functional change in the oviposition habits, and to see whether this association has had any relevance in the adaptive radiation of the genus. Most acridoids oviposit in soil (hypodaphic), although exceptions to this rule are known (Uvarov, 1977). Within Dichroplini, oviposition on the exposed surface of plants has been recorded only for species of *Scotussa*. *Scotussa cliens*, *S. liebermanni*, and *S. daguerrei* oviposit on the surface of plants (epiphytic), mainly on species of *Eryngium* (Apiaceae) and *Panicum* (Poaceae) (Liebermann, 1951; Zolessi, 1958; Cigliano & Ronderos, 1994), and *S. lemniscata* on the bases of grasses (epidaphic) (Cigliano & Ronderos, 1994).

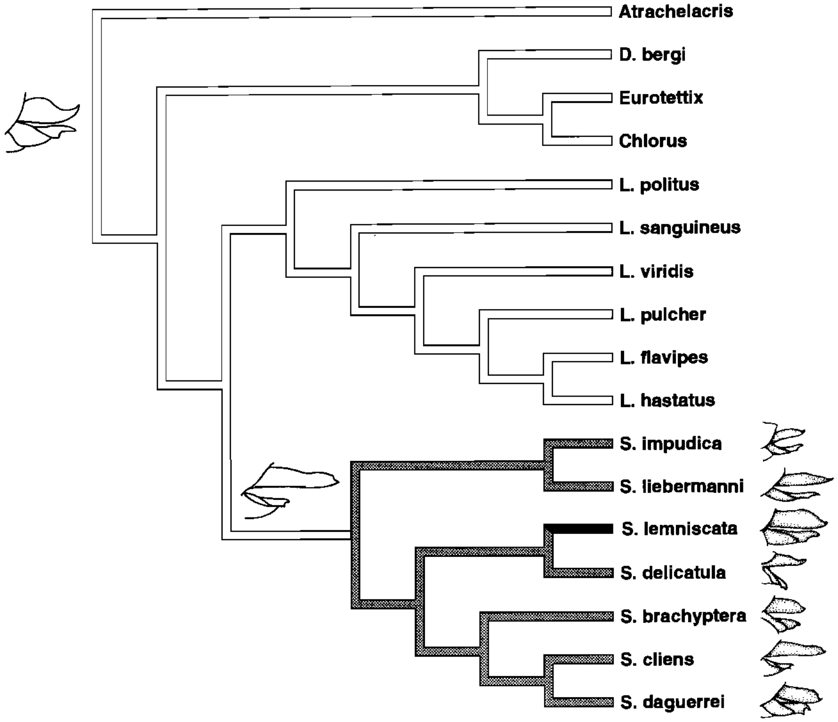


Fig. 11. Cladogram of the grasshopper genus *Scotussa* and its closest relatives (*Leiotettix, Chlorus, Eurotettix, Dichroplus berg*i species group, and *Atrachelacris*) with the ovipositor valves and indication of the sequence of performance on the oviposition habits. Hypodaphic= branches in white; endophytic= branches in grey; epiphytic= branches in black.

In order to check the performance of characters from the female ovipositor of *Scotussa,* two analyses were conducted: one where characters from this structure were excluded, and another including characters from both the external morphology and ovipositor. In order to check if any of the ovipositor characters could be parsimoniously optimised in more than one way, both DELTRAN and ACCTRAN optimisation procedures were used. The information on the oviposition habits was then mapped onto the cladogram to determine the transformation sequence for performance. The analyses yielded congruent hypotheses of relationship (Fig. 11), which support the association between the structural change that occurred in the ovipositor valves of *Scotussa* with the functional change in the oviposition habits. The structural change in the ovipositor valves of *Scotussa*, from a curved ovipositor with convergent dorsal valves to a straight ovipositor with divergent dorsal valves, is thus associated with the functional change in the oviposition habits from hypodaphic to epiphytic (Fig. 11). Such association, however, did not seem to have any relevance for an adaptive radiation of the genus, if this concept is equated with speciation rates *per se*. Even though a high degree of structural diversification on the ovipositor is observed in *Scotussa*, it is not correlated with an unusually high species diversity when compared with its sister group, *Leiotettix* (Fig. 11). Finally, although *Scotussa* is sympatrid for most of its range with the remaining taxa analysed, it reaches more southern latitudes, extending well in the Pampas south of parallel 34° S where it is largely diversified, and reaching Patagonia where no other member of the group is distributed.

## DIVERSIFICATION OF ADAPTIVE CHARACTERS

Brooks & McLennan (1991) postulated that those adaptive changes that occurred early in the ancestor of a group might constitute the step that led to unusually high speciation rates in descendant species. The result would be a species-rich clade whose members share a "key innovation", which would explain the success of the group. Sister group comparisons have been used to investigate the hypothesis that a novel trait was associated with the diversification of a clade (Mitter *et al.* 1988; Farrell *et al.* 1992). According to Miles & Dunham (1993) the procedure consists of three steps:

(1) Specify all monophyletic groups that have independently evolved the novel trait.

(2) Determine the sister groups that lack the trait.

(3) Compare patterns of species richness, ecological breadth, or other measure of diversification between the sister groups.

Thus, the species diversity of a lineage in which a new adaptation has arisen is contrasted to that of its sister group, which by definition has had equal time for speciation and extinction and should differ in the fewest other characteristics (relative to other more distantly related groups).

**Case study.** Within the family Curculionidae, which is included in the superfamily Curculionoidea (Coleoptera), the development of a sexually dimorphic rostrum, employed by the female to excavate an oviposition site in living angiosperms, has been considered a "key innovation" associated with its high species diversity (Anderson, 1993, 1995). Kuschel's (1995) cladogram of the Curculionoidea is herein used to illustrate the association between the rostrum used to excavate an oviposition site and the differential diversification in this taxon. It must be pointed out, however, that some of the relationships depicted in this cladogram have been challenged recently by some authors (Thompson, 1992; Marvaldi, 1997; Morrone, 1998), and that oviposition behaviour is more complex than it was previously assumed (Howden, 1995).

After mapping the character "endophytic oviposition in living angiosperms" onto the cladogram (Fig. 12), we can examine the number of species in each clade (as detailed in Kuschel, 1995), which provides a relative measure of the species diversification. Within Curculionidae, the clade comprising the five subfamilies where the sexually dimorphic rostrum (longer in female than male) appears, comprises 59% of the species of Curculionoidea, which makes a strong case in favour of diversification due to a change in habits or morphology. Females of these species use their long rostrum for excavating an oviposition site in living plant tissues (= endophytic) of angiosperms, where eggs are posteriorly laid. In contrast, more basal Curculionoidea do not use their rostrum in oviposition site preparation (Nemonychidae and Anthribidae) or oviposit basically on gymnosperms and ferns (Belidae, Attelabidae, and Brentidae), although some exceptions are known (Anderson, 1995; Howden, 1995).

The ancient fossil record (Kuschel, 1995), the repeated association of several Nemonychidae, Belidae, and Brentidae with gymnosperms (Anderson, 1995), and the relictual austral distributional patterns of basal Curculionoidea (Morrone, 1996) support an early origin of this superfamily, predating both the breakup of Gondwanaland and the origin of angiosperms. The use of the rostrum for oviposition in living angiosperms allowed a change in weevil oviposition behaviour, providing a better protection for the eggs and supplying plant tissues for the nourishment of the newly hatched larvae. Anderson (1995) considers that the association of the ancestors of Curculionidae with the ancestors of angiosperms, by means of the morphological change in the rostrum structure and the oviposition behaviour associated to it, allowed their diversification.

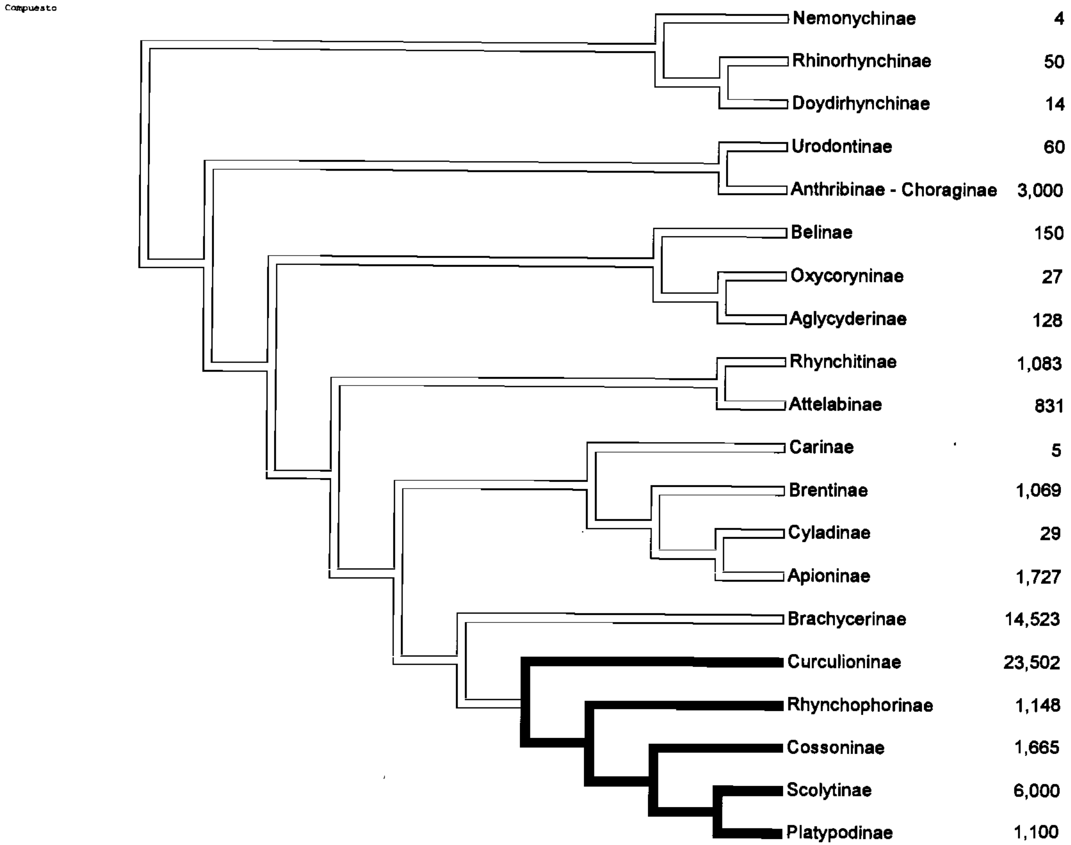


Fig. 12. Cladogram of the subfamilies of Curculionoidea (after Kuschel, 1995), with indication of the number of species per subfamily. Endophytic oviposition in living angiosperms= branches in black.

## DISCUSSION

The use of cladistic hypotheses to test hypotheses of adaptation has recently been criticised on the grounds that the cladistic approach can only test hypotheses about patterns but not about the evolutionary processes that shaped these patterns (Lauder *et al.*, 1993; Frumhoff & Reeve, 1994; Leroi *et al.*, 1994). In addition, Grandcolas *et al.* (1997) warned about the possible biases in the comparisons of the results provided by these tests in different clades, which could be related to the delimitation of characters and ingroups.

Lauder (1981) stated that the application of the sister group approach to adaptive radiation has to be taken with caution because of the following reasons: (1) each branch on the cladogram may be characterised by more than one apormorphy, so there is no way to determine which of those is the key innovation; (2) the evidence about the manner in which a key innovation enhanced the speciation rate is not strong; and (3) if the key innovation arose once, it is difficult to test whether it confers a competitive advantage.

The hypotheses of adaptation would be stronger through replication of sister group comparison if the same trait has arisen (through convergence) multiple times independently (Brooks & McLennan, 1981). These independent comparisons would allow for the statistical control for those characters that might be confounded with the trait of interest.

Even though the new methods in comparative biology do not hold the promise of being able to resolve completely questions about evolutionary processes, we can still learn a great deal about the nature of organic diversity by describing and analysing patterns of character evolution. The application of this methodology to cases like those reviewed in this paper might help point out the weaknesses in currently accepted scenarios for adaptive evolution. It may also suggest alternative explanations as well as most profitable strategies for further studies.

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