

consistency index for the most parsimonious tree should be 1.0 – that is, none of the characters evolved more than once; a case of perfect evolutionary divergence. In practice, the consistency index (or one of its more sophisticated equivalents) is seldom greater than 0.8. Maddison recently summarized the results of 38 phylogenetic analyses<sup>4</sup>. The mean consistency index was only 0.51. For the hominids the overall figure in Skelton and McHenry's analysis is 0.722. In his analysis of early hominid phylogeny Wood<sup>3</sup> had a best figure of 0.65. What this means is that, in even the most parsimonious trees, very large numbers of characters evolve convergently in different lineages, both closely and distantly related.

Cladistics has been controversial as a system for phylogenetic reconstruction, but ironically what is most interesting here is what it tells us about the process of evolution.

Parsimony analysis provides us with a crude measure of the frequency of convergence, revealing it to be a common and normal part of the evolutionary process for hominids as much as anything else. From the perspective of evolutionary ecology this is perhaps reassuring, as it is a conventional expectation of darwinism that the same environmental problems should give rise to similar adaptive solutions among small isolated populations. That this should have been the case among widely scattered hominid populations in Africa over 2 million years ago suggests that at this stage hominids were evolving like any other taxonomic group. Diversity becomes an expectation of early hominid evolution, and parsimony a problem – the complete reverse of the situation 20 years ago.

What is good news for the palaeoecologists, though, may be more worrying for those recon-

structing our evolutionary tree. Most cladistic analyses work on the principle of evolutionary parsimony. The best phylogeny is essentially the one that has the least convergence. And yet if cladistics is itself showing that convergence is rife in the real world of evolution, then the very assumptions of cladistics are open to question. In revealing elegantly how frequently selection can lead different species to parallel each other's trajectories, cladistics may well be mapping its own methodological limits.

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## Character Displacement and Replicate Adaptive Radiation

Dolph Schluter and John Donald McPhail

*Ecological character displacement is implicit in current views of adaptive radiation, but examples are few. The paucity of cases may be partly a problem of detection: statistical tests require that a consistent pattern of displacement be observed over independent lineages, yet opportunities for such replication may be few. Recent studies of fish in postglacial lakes and lizards on Caribbean islands reveal multiple speciation events accompanied by equivalent patterns of ecological and morphological divergence. These studies provide a wealth of new examples of apparent character displacement, and show that adaptive radiations may unfold in a predictable sequence.*

Adaptive radiation is the evolutionary diversification of a lineage across a variety of resource types<sup>1,2</sup>. Among the suspected causes of the process is competition between species for resources: divergence of new species in morphology and resource use is hypothesized to be driven by competition between them for food, and facilitated by an absence of competition from species in other taxa<sup>1–7</sup>. Phenotypic evolution wrought or maintained by

interspecific competition is termed ecological character displacement<sup>7–9</sup>; hence, character displacement is implicit in current views of adaptive radiation.

Whereas adaptive radiation has abundant examples<sup>1</sup>, well-supported demonstrations of character displacement are embarrassingly few (see Ref. 10 for a recent review). This could mean that the importance of the process has been overestimated, and that our concept of adaptive radiation needs to be greatly revised. Alternatively, there may be too few opportunities in nature to observe or study character displacement, despite its possible prevalence. To demonstrate the process, one must show that a given species has affected the direction of evolution in one or more competitors. Differences between sympatric sister species in morphology and resource use may potentially result from character displacement, but they constitute

weak evidence on their own because even a 'null' process of speciation and divergence could have the same outcome<sup>11</sup>. Consequently, replication is crucial to detecting character displacement; to rule out chance, evidence is needed that divergence in morphology and resource use occurs repeatedly over statistically independent lines. Yet, historical and geographical circumstances may rarely permit such independence.

Here we summarize recent examples of adaptive radiation in which similar morphological and ecological shifts have evolved multiple times under similar circumstances. Together with additional evidence, the patterns affirm character displacement as a driving force in diversification. Further study of these systems would help clarify the ecological forces that shape diversification generally, and that cause adaptive radiations to unfold in a specific sequence.

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**Speciation in fishes of postglacial lakes**

The new forms of northern hemisphere fishes evolving in lakes formed after the glaciers receded 10 000–15 000 years ago comprise a remarkable list of replicate diversification events via apparent character displacement (Fig. 1). In a wide diversity of fish taxa, speciation and divergence has yielded sympatric pairs of species that differ in size and shape, and that partition lake resources in a very consistent way. In every known case, one of the sympatric species is limnetic, exploiting plankton in the open water, and the other is benthic, consuming macroinvertebrates and other large prey chiefly from vegetation or the sediments. Different species pairs are characterized by common morphological features: the limnetic species is typically smaller, has a more narrow mouth, and has longer, more numerous,

gill rakers than the benthic species (Box 1). These morphological differences are correlated with differences in feeding performance in the two habitats<sup>12</sup>.

Three types of evidence implicate character displacement in the evolution of these species pairs. The first is the extraordinary parallelism between separate fish lineages in the ecological and morphological differences evolving in sympatry. Even characteristically benthic taxa such as the round whitefish (*Prosopium*), and otherwise planktivorous taxa such as ciscoes (*Coregonus sardinella* complex and *C. artedii* complex), have formed benthic–limnetic pairs in these postglacial lakes (Fig. 1). The sympatric fish species usually differ significantly in gill raker number and length, with the planktonic form invariably exceeding the benthic. Averaged across taxa, the separation in gill raker number between sympatric species is 4.6, or 2–3 within-species standard deviations. This separation is consistent across a wide range of taxa differing in the absolute number of rakers, as shown by a slope of 1 in the regression of Fig. 1. However, this difference can be as little as two rakers in some cases and as much as 10 rakers in others. The causes of the variability are unclear.

Second, sympatric species may be more divergent than the same or closely related species living alone nearby. For example, stickleback species (*Gasterosteus aculeatus* complex) occurring alone in small lakes of coastal British Columbia, Canada, tend to be morphologically intermediate between the limnetic and benthic species (Fig. 2) and exploit both plankton and benthos<sup>13</sup>. Solitary lake whitefish (*C. clupeaformis* complex) are intermediate in gill raker number between sympatric species<sup>14</sup>. Shifts are also evident between more distantly related sympatric fish species. For example, the single species of lake whitefish present in most Alaskan lakes have fewer gill rakers when planktivorous ciscoes are present than when ciscoes are absent<sup>14</sup>.

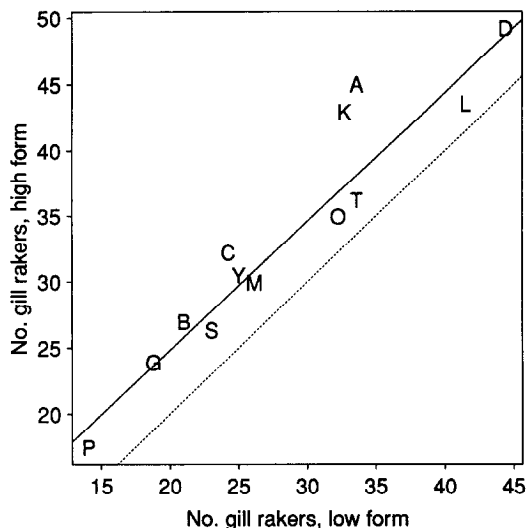
Third, formation and coexistence of species pairs may be facilitated by an absence of potentially competing fish lineages. For example, lake whitefish (*C. clupeaformis* complex)

occur as two sympatric species only in lakes in which ciscoes, specialized planktivores, are absent<sup>14</sup>. The applicability of such patterns to other groups is not yet known.

The summary of examples (Fig. 1) underestimates the number of independent cases, since multiple points from a given species pair were lumped together, yet they may represent multiple divergence events. For example, the geological history of coastal British Columbia, Canada, hints that freshwater sticklebacks have diversified independently in different drainages<sup>13</sup>. Recent mtDNA studies reveal separate origins of species pairs of smelts (*Osmerus*) occurring in different lakes of eastern Canada<sup>15</sup>.

The vast majority of sympatric species (Fig. 1) are probably true species by the biological definition rather than different morphs of a single species, although this has not yet been confirmed in all cases by behavioural or genetic studies<sup>15–20</sup>. Interestingly, known examples of single-species dimorphisms in pumpkinseed (*Lepomis gibbosus*)<sup>21</sup> and bluegill sunfish (*L. macrochirus*)<sup>22</sup> parallel species pairs in the ecological and morphological differences reported. This resemblance leads to the question of whether species pairs evolved from single species dimorphisms via sympatric speciation<sup>23</sup> or whether instead speciation occurred allopatrically. Genetic study of lake whitefish (*C. clupeaformis* complex) in eastern Canada and northern Maine, USA, shows that sympatric species formed in separate ice age refugia<sup>19</sup>. The pair of species of arctic char (*Salvelinus alpinus* complex) in Scottish lakes also appear to have formed in allopatry<sup>20</sup>. However, sympatric smelts are sometimes more similar genetically to one another than to populations elsewhere<sup>15</sup>, leaving open the possibility that they evolved sympatrically.

The above survey suggests the benthic–limnetic split to be a predictable first step in the diversification of many fish taxa in low-diversity postglacial lakes. It would be interesting to know whether this predictability would hold at later stages in the adaptive radiation. Unfortunately, few of the existing sets of three and four sister species



**Fig. 1.** The mean number of gill rakers in fish species pairs of Northern hemisphere post-Pleistocene lakes. The x-axis is the number of rakers in the species having the lower count (the benthic), and the y-axis is that in the species having the higher count (the planktivore). The solid line is the reduced major axis, and the slope is close to 1 (1.02). Dashed line is  $y = x$ . All pairs are apparently closely related sister species coexisting without other closely related species. Points may be averages of measurements from several studies on the same species complex. Ciscoes [*Coregonus (Leucichthys)* A, D, and L] were treated separately from other *Coregonus* (M, Y, C, T). *Coregonus clupeaformis* in Yukon and Maine were treated separately, because electrophoresis suggests that the species pairs in the two areas are independently derived<sup>14</sup>. Symbols from left to right are: P, *Prosopium coulter*<sup>31</sup>; G, *Gasterosteus aculeatus*<sup>13</sup>; B, *Brachymystax lenok*<sup>32</sup>; S, *Salvelinus alpinus*<sup>18,20,33–36</sup>; C, *Coregonus lavaratus*<sup>14,37,38</sup>; Y, *C. clupeaformis* in Yukon lakes<sup>14</sup>; M, *C. clupeaformis* in Maine lakes<sup>39</sup>; O, *Osmerus*<sup>15</sup>; T, *C. tugun*<sup>40</sup>; K, *Oncorhynchus nerka*<sup>16</sup>; A, *C. albula*<sup>37</sup>; L, *C. sardinella*<sup>41</sup>; D, *C. artedii* (data from Ref. 42 and R.M. Clarke, unpublished PhD dissertation, University of Manitoba, 1973).

are well described, and this makes comparison difficult. The three forms of brown trout (*Salmo trutta*) in Irish lakes include a benthic form, a planktivore and a piscivore<sup>24</sup>. However, the three species of round whitefish (*Prosopium*) in Chignik Lake, Alaska, include no piscivore, but a planktivore and two benthivores, one living at greater depth than the second<sup>14</sup>. The same has happened independently in the three round whitefish species of Bear Lake, Idaho<sup>25</sup>. Perhaps the divergent triplets would converge at the four-species step, as suggested by the four known forms of arctic char in an Icelandic lake (these may represent a single-species polymorphism rather than four separate species): a planktivore, two benthivores (one living at greater depths than the other) and a piscivore<sup>26</sup>.

**Repeatable steps in adaptive radiation of *Anolis***

Deducing the sequence of diversification events in a lineage is straightforward when only one or two species are present. However, past events in more diverse lineages are becoming accessible with the new tools of phylogenetic analysis. The first attempt to compare the sequence of events in two lineages using these methods was recently carried out by Losos<sup>27</sup> on West Indian *Anolis* lizards.

The analysis centred on the separate adaptive radiations of *Anolis* on the islands of Jamaica and Puerto Rico. The various species fall into simple ecological groups on the basis of their microhabitat and morphology, which are strongly linked through morphology's effect on locomotor performance<sup>27</sup>. Jamaica has four of these morphs: Twig, Trunk-ground, Crown-giant, and Trunk-crown. Puerto Rico has these same four plus one more, the Grass-bush morph. On each island, a morph usually consists of only one species of *Anolis*, although Puerto Rico has three Trunk-ground and three Grass-bush species. Each trio is closely related, and the three species tend to occupy different habitats<sup>5</sup>. The phylogenies of the morphs are shown in Fig. 3.

Species of the same ecological morph on different islands have virtually the same body shape (e.g.

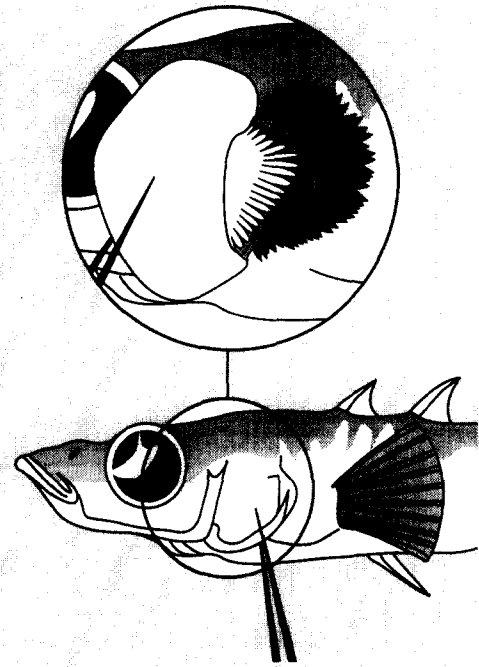
**Box 1. Gill rakers and their function**

Gill rakers are cartilaginous spines occurring in rows along the gill arches of fish [magnified portion of diagram shows the operculum of the fish lifted and folded aside, revealing the first gill arch beneath, and its gills (right) and rakers (left)]. These structures are generally long and closely spaced in planktivorous fish, and are reduced and more widely spaced in benthic species or other types feeding on larger prey. A reasonable hypothesis is that the series of rakers functions as a sieve, intercepting plankton from the stream of ingested water exiting the oral cavity through the gill arches. However, the true function of rakers is probably more complex, since many planktivores are able to consume items much smaller than the spaces between adjacent rakers. Also, species that do not feed on plankton nevertheless retain an array of rakers, which, though reduced in number and length, presumably still have some function.

Sanderson and co-workers<sup>43</sup> recently presented a novel proposal for the function

of the rakers. Using a fiberoptic endoscope and flow probe inserted into the oral cavity of feeding blackfish, they observed that rakers acted as a barrier to water flow rather than as a filter. Ingested prey were carried by currents flowing between the rows of rakers to the roof of the oral cavity, where they were trapped by mucus before being swallowed. The blackfish is a highly specialized planktivore, and it is not known whether rakers function similarly as a barrier in other species. However, it is likely that rakers generally influence water currents in the mouth, though how they do so is not yet known for most fish.

It should be possible to directly measure the contribution of rakers to feeding performance by surgically deleting them. Such a manipulation was carried out<sup>44</sup>, but the results were ambiguous. Feeding success on small items of plankton was not significantly reduced after rakers were removed. However, estimates of particle ingestion rates of treated and control fish were highly variable, and even the possibility that surgery enhanced feeding efficiency could not be ruled out. Further measurements are awaited.



relative lengths of hindlimbs and forelimbs). This made it possible to identify the ecological characteristics of species present at each stage of the two adaptive radiations by estimating the morphologies of all ancestral species (Fig. 3). These estimates are based on the assumption of parsimony: that the total amount of morphological evolution that took place during the radiations was minimized<sup>28</sup>. The uncertainties of these estimates is not yet known (i.e. there are no confidence intervals or 'parsimony intervals'), but they provide a good first look.

The results suggest that the branching sequences were not identical on the two islands (Fig. 3); for instance, the Crown form was never itself an ancestor on Jamaica, unlike Puerto Rico. Yet, at each step of the radiations, the communities were composed of very similar sets of morphs. The Grass-bush morph was the last to evolve on Puerto Rico, from a Trunk-ground-like ancestor; hence, lizard communities at the four-morph stage were identical. The same was true at each preceding stage (Fig. 3).

The evidence for character displacement in these Greater Antilles lizards is not based on the standard comparison of differences between species in sympatry and allopatry (e.g. Fig. 2). Instead, it lies in the near-perfect ecological matching between species sets on different islands (Fig. 3), and the fact that evolution has proceeded independently in a similar sequence. In no case did a morph already present on an island evolve again in a later step, suggesting that, once filled, a niche is less likely to be invaded a second time.

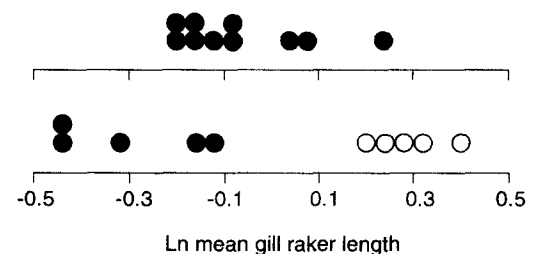


Fig. 2. Mean gill raker length in sympatric (lower) and solitary (upper) forms of three-spined sticklebacks (*Gasterosteus aculeatus*) in small lakes of coastal British Columbia, Canada. Circles indicate means for benthics (filled), limnetic (open) and solitary (shaded) populations. Data from Ref. 13.

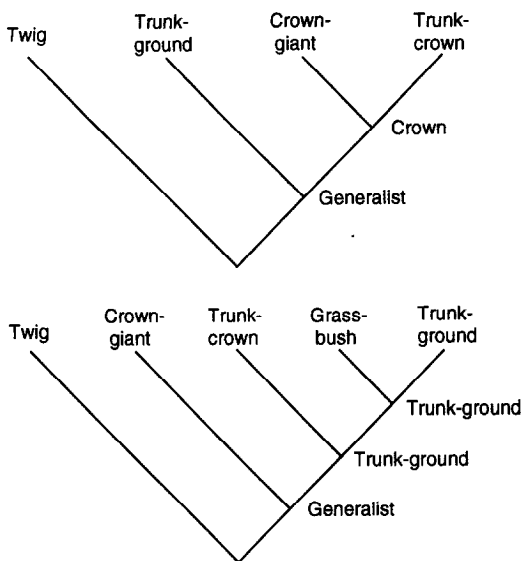


Fig. 3. Phylogenetic relationships among the ecological forms of *Anolis* lizards on Jamaica (upper) and Puerto Rico (lower). Labels at nodes in the tree are the estimated ecological characteristics of the ancestors. After Ref. 27.

Losos' study forecasts more comparisons of the ecological histories of lineages, especially more distantly related ones. For example, Richman and Price<sup>29</sup> recently used phylogenies to estimate the sequence of ecological transitions in the radiation of a group of Old World leaf warblers (*Phylloscopus*). Their study begs a comparison with the convergent New World warblers (*Parulidae*).

**Conclusion**

From the Cambrian explosion to the radiation of mammals, life's history seems largely to be a catalogue of unique events. We have surveyed some recent studies in which circumstances conspire to yield a level of repeatability in adaptive radiation not heretofore recognized. The cases provide a wealth of new examples of apparent character displacement, and opportunities to probe further the general origins of diversity. The very young history of the interactions between many of the fish species also suggests the interesting possibility that evolutionary processes favoring divergence are still at large, and might be observed directly through careful field study.

The patterns strongly suggest a controlling influence of resource availability and interspecific competition on patterns of evolutionary diversification. Further work on these systems will need to test the mechanism of competition, and measure its importance in relation to other possible interactions be-

tween species such as intraguild predation. Also, we do not yet understand why at each step of diversification resource availability and competition would favour divergence in some directions and not others (why limnetic versus benthic so often instead of benthic versus piscivore?). Finally, we need to evaluate alternative possible explanations for these patterns. For example, is it possible that the repeated evolution of differences in gill raker number and habitat illuminated in Fig. 2 reflects developmental constraint rather than ecological setting? This possibility could be addressed by asking how diversification proceeds in the same lineages but in different environments (e.g. streams instead of lakes, where the plankton niche is lacking).

These recent adaptive radiations suggest that to a certain extent evolution is repeatable. This would seem to contradict the principle that chance and historical contingency would foil any repetition of life's history<sup>30</sup>. Yet, we expect some repeatability to occur, since there are a limited number of resources available anywhere, and in some cases a limited number of designs that would work to exploit them. Hence, if we were to scour the earth of all of its vertebrates, some other kind of organism would probably eventually evolve to fill the void. And though the precise virtues of a creature such as the stickleback would never be duplicated, we strongly suspect that the new faunas would include limnetics and benthics.

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