The study of innovation occupies a central position within evolutionary biology. The concept of evolutionary innovation, or novelty, has been interpreted in many different ways by biologists, but it is probably accurate to say that most understand innovations to mean the appearance of new characters or structural/functional complexes. These innovations are found to characterize individual organisms within a population, basal species-level taxa, or they are shared by clusters of species, which may or may not comprise a monophyletic group. Generally, however, biologists have discussed the evolutionary significance of innovation within the context of large-scale manifestations of the phenotype, particularly those morphological, behavioral, or physiological traits that are interpreted to facilitate a new way of making a living and that somehow are thought to be causally related to the success of the major taxonomic group possessing them. Thus, Mayr (1963:602) has defined evolutionary novelty "as any newly acquired structure or property that permits the performance of a new function, which, in turn, will open a new adaptive zone." A similar conception of evolutionary innovation is echoed by many within the evolutionary literature. The list of identified novelties is endless, virtually equaling the diagnostic characters of all successful higher taxa. Some of those most often mentioned as "classic" examples of evolutionary innovation include: the bony skeleton of vertebrates, jaws of gnathostomes, the amniote egg, avian flight, feathers, continuously growing incisors
of rodents, large brain of hominoids, the artiodactyl tarsus, the insect wing, rigid skeletons and complex spicules of sponges, and the insect pollination system of angiosperms.

The study of innovations has occupied center stage within evolutionary biology for a number of reasons. Perhaps the most important has been the desire of biologists to explain the apparent design of organisms by relating the structural/functional characteristics of these innovations to particular ways of life using the conceptual framework of adaptationism. Such an exercise, it is often suggested, informs us as to how and why the particular innovation originated and was increasingly perfected as adaptive design. That this conceptual framework has dominated the study of innovations is easily demonstrated by recasting it in terms of its converse and compiling a list of all those innovations that are considered to be less efficient or less well designed functionally relative to the more primitive condition. Whether or not such innovations exist, biologists have seldom conceptualized the problem in this way. As a result, that list would be short indeed (even reductions or vestigial structures are regularly given an adaptive interpretation).

A second major reason why the study of innovation has been considered so important is the conjecture that innovations are causally related to the evolutionary success—in terms of diversity or historical persistence—of clades. The concept of "key innovations" continues to play a prominent role in explanations of this type, and all the examples just given have been identified, by one or more authors, as key innovations.

This chapter will evaluate the concept of key innovation and assess the proposition that these features are causally important in explaining patterns of diversification. The discussion of these subjects will be organized around three main themes, one ontological, one methodological, and the third empirical:

1. The ontological theme. A substantial proportion of the key innovations noted in the evolutionary literature are typological constructs. Empirically they do not represent true evolutionary innovations, and as such are
limited in what they can tell us about the processes actually responsible for the origin and maintenance of evolutionary novelties. The ontological mistake has arisen because the analysis of evolutionary innovation has largely been confined to hierarchical levels well above that at which processes producing innovations have operated.

2. The methodological theme. A more rigorous methodological approach to the study of innovation is required, one that begins at the hierarchical level of speciation analysis and extends downward to molecular developmental genetics. Manifestations of pattern above the level of differentiating populations, or basal taxa, are epiphenomena, or effects, of lower level processes.

3. The empirical theme. A conjecture will be proposed: the role ascribed to key innovations as being causally related to patterns of diversification must be largely incorrect. This is not to say that innovation, analyzed at its proper hierarchical level, has no influence on the subsequent history of a group, but that the causal connections are complex. Partitioning different patterns and processes into their proper hierarchical levels will help resolve these complex causal connections.

The Historical Anatomy of a Key Innovation: Avian Flight

Structural complexes are typically identified as key innovations because, first, they are characteristic of, or correlated with, a monophyletic taxon of high diversity, and second, they are judged to be functionally important in the way of life of species in that taxon. Most important, perhaps, is the supposition that the innovation itself caused the high diversity. The origin of avian flight is frequently identified as one such innovation (Mayr 1963:598; Futuyma 1986:356) and can serve as an exemplar of most kinds of key innovations discussed in the literature. One approach to understanding the possible role key innovations may have played in the success of a group is to examine the
*historical structure* of the putative innovation within the context of a phylogenetic hypothesis for the group and its close relatives (see also Lauder 1981; Larson et al. 1981; Stiasny and Jensen 1987; Lauder and Liem, in press).

The cladistic pattern of early avian relationships is becoming better understood and can be used to reconstruct the historical structure of avian flight. The phylogenetic hypothesis of figure 1 is based on numerous characters, including some not directly associated with flight (Cracraft 1986, 1988), but only those characters comprising the flight apparatus will be considered here. Without belaboring the point, categorizing structures as part of something called the "flight apparatus" is often arbitrary. Many modifications of the vertebral column, pelvis, and hindlimb undoubtedly have been important functional components of avian flight since their inception, yet they will be omitted from this discussion.

The relationships between birds and one or more groups of theropod dinosaurs is now well established (Ostrom 1976; Padian 1982; Gauthier and Padian 1985; Gauthier 1986), and present evidence suggests that the sister group of birds is the Deinonychosauria (Gauthier 1986). Within the context of this phylogenetic hypothesis, then, it is apparent that some characters of the flight apparatus arose prior to node 1 of figure 1, including elongated forelimbs, a thin and bowed metacarpal III, and, most probably, an ossified sternum (Gauthier 1986). Features postulated to have arisen at the hierarchical level of node 1 include feathers, loss of fusion between the scapula and coracoid, rotation of the forelimb so that the elements can assume a typical avian resting position (Martin 1985), and an enlarged forebrain, midbrain, and cerebellum. *Archaeopteryx*, it should be pointed out, was almost certainly capable of true powered flight.

Avian remains recently discovered in the Lower Cretaceous of Spain (Sanz et al. 1988) seem to represent a taxon that is the sister group of all birds excluding *Archaeopteryx*. That clade (fig. 1, node 2) is defined by four characters associated with the flight apparatus: pygostyle, strutlike coracoid articulating with the sternum and forming a brace for the pectoral girdle and
forelimb, a procoracoid process on the coracoid, and a shift in the scapulocoracoid articulation to a position below the distal end of the coracoid.

At the level of *Hesperornis* and the Carinatae (fig. 1, node 3), no characters involved in flight are known to have arisen. *Hesperornis* was secondarily flightless, and the forelimb was structurally simplified. In contrast, the Carinatae (fig. 1, node 4) are characterized by a number of features that are components of the flight apparatus: a keel on the sternum, a carpometacarpus, the external condyle of the ulna developed as a semilunate ridge, and a humerus with a strongly developed internal tuberosity, strongly defined head and distal condyles, brachial depression, and a pneumatic fossa and foramen.
No new features of the flight apparatus have been shown to characterize the Neornithes or modern birds (fig. 1, node 5), though some undoubtedly exist.

Traditional descriptions of avian flight as an evolutionary innovation begin with *Archaeopteryx* and a modern flying form and create a scenario of how the structural features of *Archaeopteryx* might have been transformed by natural selection into those of a modern flying bird. This is not meant to imply that these workers envisioned all characters to be changing uniformly through time, but without a cladistic hypothesis for all relevant taxa the historical pattern of character innovation cannot be reconstructed.

Even though the majority of discussions of key innovations have been undertaken in the absence of a cladistic analysis, there are other more serious problems with traditional analyses. First, it is readily apparent that the key innovation just discussed lacks any ontological status as an evolutionarily discrete novelty. Avian flight, even if it could be said to characterize modern birds, is composed of a very large suite of characters that arose within the avian clade at very different times, extending over perhaps 50 million years or more. In addition, many of the "characters" just discussed are undoubtedly themselves aggregates of characters, which arose at different times (e.g., "feathers"). Most, if not all, of the "key innovations" listed earlier lack ontological status as discrete evolutionary novelties.

It is also important to realize that hypotheses about the sequence of origination for these characters are dependent upon the taxic sample and the phylogenetic information specified by all other characters in the analysis. In an analysis of avian flight, for example, a large number of cranial and postcranial characters contribute to establishing the phylogenetic hypothesis and thus have a marked influence on how the characters of the flight apparatus are interpreted historically.

An example such as this raises two additional difficulties for the analysis of key innovations. The first is that extinction has been rampant and it has torn apart the phylogenetic nexus, leaving a seriously inadequate sample of taxa and their accompanying characters; this sample constitutes the only
evidence we have to reconstruct the history of any key innovation. This difficulty is magnified by another, namely, that a causal analysis of the evolution of key innovations must be at the level of species or below (e.g., Larson et al. 1981). Processes contributing to the evolution of novelties do not have direct causal effects at levels above the species, and thus most analyses of key innovations, which investigate patterns among supraspecific taxonomic units, are descriptively inadequate purely as a consequence of extremely poor sampling of species-level taxa in the historical record. Nearly all of the "key innovations" noted above would undoubtedly fall into this category.

To emphasize these latter points, it is worthwhile reviewing the mechanisms by which evolutionary innovations arise and become established.

The Origin of Innovations: Intersection of Two Hierarchical Levels

The preceding discussion made the ontological claim that most so-called "key innovations" are not true evolutionary innovations but are instead aggregations of these innovations, which arose sequentially over vast stretches of time. In order to establish a more precise ontology for investigating questions about the causes responsible for the origin and subsequent history of innovations, we need to define some terms explicitly.

1. *Prospective innovations* are singular phenotypic changes that arise in individual organisms within a population as a result of a modification in one or more ontogenetic pathways.

2. *Evolutionary innovations* are singular phenotypic changes that, subsequent to arising in individual organisms, spread through a population and become fixed, thus characterizing that population as a new differentiated evolutionary taxon.

To make these definitions general, changes from the molecular level to that of adult physiology, behavior, biochemistry and morphology could be included within the context of "phenotypic." The important distinction to be
made, however, is between the hierarchical level at which causal processes operate to establish innovations and those at which various processes might determine their historical fate. Given the conception of innovation implied by the preceding definitions, a mechanistic description of the origin of prospective innovations will lie within the domain of molecular biology and developmental genetics (e.g., Bonner 1982; Raff and Kaufman 1983; John and Miklos 1988), whereas a mechanistic description of the origin of evolutionary innovations will be found within the domain of population biology.

Most importantly, perhaps, once evolutionary innovations become established in a population so as to characterize it as a new evolutionary taxonomic unit, or species if you will, then, above that hierarchical level, patterns involving these innovations are interpretable as epiphenomena or effects. Arguably, there are no processes above the level of differentiating populations that determine the origin or establishment of evolutionary innovations, but there may be higher-level processes that determine the relative frequency of those innovations as expressed as patterns across space, time, and among taxonomic groups. To speak of macroevolutionary processes as those that account for large-scale innovations defining higher taxa (e.g., Alberch 1982:313; Gould 1982:340; Levinton 1988:2) misrepresents the hierarchical level at which processes producing innovation are located. Irrespective of whether innovations are perceived as "large" or "small," they all must arise and become established at the levels of individuals and populations, not higher taxa.

This discussion implies that the correct domain for studying innovation is between the molecular (processes of mutation and development) and populational (processes of differentiation) levels and that the approaches brought to bear on the problem of innovation will depend upon the questions asked and the focal level to which they are directed. Partitioning patterns and processes into their appropriate hierarchical levels also implies that the analysis of speciation will become increasingly important for the study of evolutionary innovations. It also suggests that a methodological protocol for the study of evolutionary innovation needs to be developed (see also Lauder and
Speciation and Innovation: A Suggested Protocol

Evolutionary innovations are those fixed in basal evolutionary taxonomic units, and ideally it would be desirable to have a historical record of all the novelties—whether molecular, physiological, or morphological—manifested as differences among these taxa. Accordingly, a protocol for the historical analysis of evolutionary innovations will have the following four elements:

1. Delineation of basal differentiated evolutionary units. Processes of taxonomic differentiation result in populations that are diagnosably distinct from other such populations. Hypotheses about the boundaries of these basal taxa can therefore be formulated on the basis of a comparative analysis of discrete character variation, that is, of observable evolutionary innovations (Nelson and Platnick 1981; Cracraft 1983, 1987).

2. Exhaustive sampling of evolutionary innovations. At the level of basal taxa, diagnostic characters are evolutionary innovations. In the ideal case, we would like to have an exhaustive list of these characters for all basal taxa. In general, however, the kinds of innovations sampled and the extensiveness of the sampling effort will depend upon the questions being asked. Two types of characters must be sampled: those shared by basal taxa and those diagnostic of each basal taxon in the analysis.

3. Erection of a phylogenetic hypothesis for the basal taxa. A cladistic hypothesis will apportion postulated evolutionary innovations most parsimoniously across the tree. Indeed, without a phylogenetic hypothesis one cannot distinguish between innovations that are shared by two or more taxa as a result of common ancestry and those that apparently arose independently. If the history of innovations is to be interpreted correctly, these two types of pattern must be distinguished.

4. Selection of clades with minimal extinction. A complete record of
evolutionary innovations can be obtained only if the clade being studied has not lost evolutionary taxa through extinction and if the investigator has sampled all the taxa. Extinction of one or more evolutionary taxa can lead to incorrect interpretations of character change, such as interpreting some characters as autapomorphies when in fact they are synapomorphies. This makes other species appear more apomorphic than they really are.

Judging the relative amount of extinction within a group is a problematic exercise at best. In some cases, a good fossil record will inform whether some taxa are extinct, but not all extinct taxa enter into the sedimentary record. And it is unlikely, particularly in terrestrial sedimentary regimes, for the record to be sufficiently fine-grained across both space and time such that all relevant evolutionary taxa will be preserved. The only other source of data potentially capable of permitting inferences about extinction is that of historical biogeography. If the clade under study has evolutionary taxa endemic in the same areas as taxa in other clades, and if these clades exhibit biogeographic congruence with respect to the phylogenetic relationships of their component taxa, then it may be possible to identify potential extinction events when taxa in some clades are missing from certain of those areas. Only two alternatives seem possible: either the taxon is present in the area but unsampled or the taxon was never present. If one could make an ecological or biogeographic argument that a species should be expected in the area in question but is lacking, then perhaps the case for extinction is strengthened. Realistically, however, it should be noted that conjectures about specific extinction events in the absence of direct evidence from the fossil record border on the ad hoc and effectively mean one’s interpretations must assume some data to be missing. The use of biogeographic evidence may be appropriate when arguing that there has been no (or minimal) extinction as, for example, when all areas of endemism are found to have an endemic species, in which case all interpretations of character evolution are derived only from known taxa. Despite our desire to know whether patterns of character distribution have been structured by extinction, precise knowledge of those influ-
ences will undoubtedly remain intractable for most groups of organisms.

This four-step protocol is a powerful tool with which to investigate evolutionary innovations. First, it helps identify innovations and establishes the hierarchical level at which they characterize one or more evolutionary taxa. This means that molecular and developmental biologists can use this historical hypothesis to discriminate between innovations and primitive retentions, and it sets the stage for interpreting developmental data historically.

Second, it permits the quantification of rates of change along different lineages. Thus, the magnitude of innovation in different evolutionary taxa can be estimated. Such information is essential if hypotheses of character evolution are to be tested. In particular, it allows us to ask whether large-scale changes in phenotype arise as evolutionary innovations, or whether most morphogenetic changes are of small phenotypic effect. More important, perhaps, it provides a method whereby the relative frequencies of these types of changes can be estimated.

Third, the method also permits the identification of historical patterns of covariance in characters. Given these patterns, many questions could be asked within the disciplines of developmental biology, functional morphology, and population biology.

Speciation and Innovation: An Example. In order to illustrate aspects of the above protocol, the pattern of speciation within a group of South American parrots will be examined. The genus *Pionopsitta* consists of at least eight basal evolutionary taxa, or phylogenetic species (Cracraft 1983; Cracraft and Prum 1988). They are distributed in nearly all of the major areas of endemism in tropical South America, and a hypothesis of their cladistic relationships is moderately corroborated using external characters (Cracraft and Prum 1988). Because there do not appear to be major distributional gaps, and because the area-relationships of the areas of endemism as specified by the cladistic relationships of these species are congruent with those of other clades of birds, a reasonable working hypothesis is that extinction in this
group has been minimal.

The innovations (characters) to be discussed include external morphological characters of coloration and color pattern (table 1), and an effort has been made to include all shared and unique characters. A phylogenetic hypothesis based on a cladistic analysis of these data (using the algorithm PAUP, Swofford 1985) is presented in figure 2. A single most parsimonious tree was found to have a length of 33 steps and a consistency index of 0.909 (there being one reversal and two cases of parallelism; see fig. 2).

This historical hypothesis forms a basis for a deeper understanding of evolutionary innovation within this clade. Some lineages and species are characterized by much more change than others. In particular, the sister

PIONOPSITTA

Figure 2. A phylogenetic hypothesis for the species in the South American parrot genus, Pionopsitta (after Cracraft and Prum 1988). Numbers refer to postulated derived characters ("innovations") listed in table 1; parallelisms are underlined and a negative sign indicates a reversal. Some lineages (e.g., the barrabandi/vulturina clade) exhibit higher rates of change, or changes with greater phenotypic effect, than their sister lineage. See text for discussion.
Table 1
Character-state data for the parrot genus *Pionopsitta* and its outgroup, *Hapalopsittaca*.

<table>
<thead>
<tr>
<th>Characters and character-states*</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
<th>20</th>
<th>21</th>
<th>22</th>
<th>23</th>
<th>24</th>
<th>25</th>
<th>26</th>
<th>27</th>
<th>28</th>
<th>29</th>
<th>30</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. melanotis</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pileata</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. haematochrous</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. coccineicollis</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pulchra</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. barrabandi</em></td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. vulgarina</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pyriola</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. caica</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Character (character-state) key (0=absent, 1=present): 1, extensive bright red wing lining; 2, extensive red on upper flank; 3, shoulder patch bright orange-red or yellow; 4, bright orange-red shoulder patch; 5, bright yellow shoulder patch; 6, upper breast yellow-green; 7, upper breast shining yellow-green; 8, belly deep blue-green; 9, tibial feathering with extensive yellow, orange, or red; 10, crown and hindneck darkish, with moderate to heavy melanin deposition; 11, crown and back of neck black; 12, crown, throat, and back of neck yellow; 13, crown bright red in male, not female (sexual dimorphism); 14, crown and upper back dirty yellow-green; 15, throat with extensive deep black; 16, red on malar and auricular; 17, yellow malar patches; 18, face extensively pinkish red; 19, head feathers reduced; 20, yellow collar around head; 21, basal portion of inner web of tail yellow (ventral view); 22, trailing edge of primaries green (ventral view); 23, breast with red; 24, red on tail (ventral view); 25, lores only partly feathered; 26, yellow-orange shoulder patch; 27, yellow tibial feathering; 28, red shoulder patch; 29, wing lining bright scarlet; 30, red tibial feathering.*
species *barrabandi* and *vulturina* are markedly distinct morphologically relative to the other species, and each has diverged significantly from their common ancestry. Indeed, *vulturina* has sometimes been placed in a monotypic genus.

These findings raise interesting questions for workers focusing at lower hierarchical levels. If it is assumed that all taxa of this clade have been sampled and there has been no extinction, then the relatively higher frequency of innovations in the *barrabandi-vulturina* lineage and in *vulturina* itself suggests that either the frequency of mutational events of small effect has increased or some mutational events have had greater phenotypic effect than in other parts of this clade. In the same vein, if it is assumed that rates of mutational events were approximately equal across all lineages, then events having a marked influence on morphogenetic pathways affecting plumage pattern and coloration were about as frequent as those having small effects (compare, for example, the numbers of innovations along each lineage).

If more were known about the developmental genetics of these characters, it might be possible to substitute strong inference for speculation. Still, examination of the patterns of covariation seems to imply that there might have been single mutational events that caused moderately extensive modification of the phenotype by perturbing morphogenetic pathways affecting the deposition of various pigments at different locations on the body. For example, two of the characters (11 and 15 of table 1) shared by *barrabandi* and *vulturina* involve deposition of melanin in feathers of the head; in *barrabandi* all three characters (17, 26, 27) include a change in carotenoid pigmentation to express yellow coloration at three different locations; and in *vulturina* a modification in carotenoid pigmentation is expressed as red coloration at several of the same locations as the changes in *barrabandi*.

The message of this example is that a protocol involving the cladistic analysis of differentiated populations, or basal taxa, is required in order to recognize innovations and define their historical pattern (see also Larson et al. 1981). Moreover, the protocol permits us to identify sister taxa and to in-
investigate historically how alterations in morphogenetic pathways might relate causally to adult differences. Only one set of characters has been sampled in this example, and others might yield different patterns. Nevertheless, the example itself is realistic in the sense that an exhaustive enumeration of all evolutionary novelties is beyond the scope of any analysis.

Key Innovations and the Causal Analysis of Diversification

Patterns of taxonomic diversification have generally been explained within an adaptationist context (e.g., Simpson 1953; Mayr 1963), and a prominent component of such explanations is the key innovation: "In general, adaptive radiations will not occur until after an evolutionary novelty has reached a certain degree of development..." (Liem 1973:426). This claim is first one of correlation and then of causality. A group of high diversity is identified and some diagnostic character or character-complex is noted and proposed to be a key innovation. By baptizing this character a key innovation, the biologist conjectures a causal relationship between the appearance of that innovation and the subsequent diversification of the group. It is worthwhile to scrutinize this claim in more detail.

Changes in diversity within a monophysletic group are the result of changes in rates of speciation and/or extinction. With respect to increases in diversity, the rate of speciation must increase relative to the rate of extinction, which can come about as the result of an increase in the rate of speciation or a decrease in the rate of extinction, or both.

Three broad categories of factors are potentially responsible for increasing the rate of speciation. The first includes those factors that increase the rate at which populations become isolated. The higher this rate, all things being equal, the higher should be the rate of differentiation. For example, an increase in geomorphological complexity would tend to increase the rate of vicariance and thus allopatry (Ross 1972; Cracraft 1985).
A second set of factors includes those that increase the rate at which novelties enter populations. These factors reside at the level of the genome and are mutational events that alter developmental pathways. Again, all things being equal, the higher the frequency of mutational events, the more variability within populations and the more likely some of that variation will become fixed.

The final set of factors includes those increasing the rate at which novelties become fixed in populations. This might entail intensification of directional natural selection or sexual selection, or it could include increases in fixation because of the influences of stochastic events (relative differences in population sizes, for instance).

How might the key innovations listed above have an influence on speciation rate? It is clear that the majority cannot. First, most lack ontological status as true evolutionary novelties. Most are composites of numerous true evolutionary novelties and are often artifacts of extinction and sampling, and artifacts cannot be causal of anything. Secondly, even if one of these innovations were a singular evolutionary novelty, the real problem would be to discover how that innovation could have increased the speciation rate of the clade possessing it as a synapomorphy. Such innovations must influence speciation through one of the three factors just mentioned. Rigorous causal hypotheses may be exceedingly difficult to formulate because they will have to be based on something other than the correlation between cladal diversity and cladal synapomorphy. Unique events, moreover, do not lend themselves to rigorous causal analysis (Lauder 1981; Stiassny and Jensen 1987; Raikow 1986, 1988): "Suppose we agree that wings are a key adaptation of bats. How can we show that they are responsible for there being ca. 870 species as against, say, 87 or 8,700?" (Raikow 1988:77). Indeed, how might we demonstrate that a "key innovation," which is present in a speciose group but not in its much less diverse sister taxon, is responsible for elevating speciation rate in the former? Three answers to this question have been suggested:
1. The comparative argument. It is claimed that causation can be inferred if we find the same novelty in unrelated taxa, all of which exhibit high diversity. Kochmer and Wagner (1988) have suggested, for example, that small body size is in some way causative of high diversity because the species of many speciose groups are comprised of small individuals. Ignoring some obvious difficulties of "small size" as a key innovation, arguments of this type identify not causation but multiple correlation. To confound matters, moreover, such "correlations" are almost always spurious because diverse "groups" are chosen a posteriori (the taxonomic artifact noted by Raikow 1988) and numerous counterexamples are inevitably ignored (for example, there are countless clades of low diversity in which individuals are of small body size: were these also used to document the "correlation"?). Even if one restricted comparisons to sister clades, it is not immediately obvious how the sample universe could be chosen without bias, short of including all sister clades, an impossible task since phylogenetic relationships for virtually all organisms are so poorly resolved. Choosing taxa of a particular rank, such as families or orders, as Raikow (1988:78) has noted, is arbitrary and thus imposes an artificiality on the data in the sense that such a procedure excludes all other clades from the sample: why choose a clade for comparison simply because it has historically been called a family or order? Why, moreover, should taxa of the same rank be considered equivalent, or comparable, across groups, or even within a relatively closely related group such as birds or mammals (see Cracraft 1981)?

2. The functional argument. Causation is inferred, first, from a correlation between some novelty and high diversity, and, second, from a conjecture that the novelty is functionally, or adaptively, important. Liem (1973) proposed, for example, that a few simple modifications of the jaw apparatus of cichlid fishes comprised a key innovation that enabled cichlids to specialize on a variety of food types in a variety of habitats and thus attain high diversity. Arguments formulated in these terms, however, are little more than restatements of the original correlation: the family is diverse and we
observe that its species are also structurally and ecologically diverse. A causal connection to speciation and extinction rates still has not been demonstrated.

The functional argument takes on the appearance of demonstrating the causal importance of key innovations when the novelty is said to be directly related to speciation or extinction rate control. One such study said to "test" (Fitzpatrick 1988) the hypothesis of a causal relationship between an innovation and speciation rate is Ryan's analysis (1986) of anuran diversity. Ryan found a correlation between complexity of an inner ear organ (the amphibian papilla) and cladal diversity. Physiological data indicate that the more complex the amphibian papilla, the greater is its sensitivity to a range of frequencies, and Ryan reasoned that "since mating call divergence is an important component of the speciation process, differences in the number of species in each lineage should be influenced by structural variation of the inner ear" (Ryan 1986:1379). The most diverse families, he observed, possess the most structurally complex form of the amphibian papilla.

It is questionable whether these kinds of data constitute a test of the hypothesis of causation. First, the link to causation basically restates the original observation: the most diverse taxa exhibit the most variation in vocal frequencies and have the most complex amphibian papilla. Because all diverse clades ("families" in this case) have the same form of the amphibian papilla, its mere presence does not directly tell us how the taxonomic diversity and its broad range of vocal behavior was generated. Second, the causal correlation may well be spurious because it is merely a synapomorphy of a diverse clade. If this character is truly causal of high diversity, one might predict that sister taxa within this large clade would have nearly equal diversity. In fact they do not. Some sister taxa having a complex amphibian papilla differ in diversity by as much as an order of magnitude (e.g., Leptodactylidae versus Dendrobatidae). If variation in the structure of the amphibian papilla is causally related to an increased speciation rate, such an inference cannot emerge in a simple fashion from observed correlations to cladal di-
versity. The fact that these sister taxa differ in diversity demonstrates that other factors underlie variation in diversity, and if other factors are operable, how do we specify — and we must if the hypothesis of causation is truly "testable" — the contribution made by the amphibian papilla? In this case at least, it seems that the hypothesis of causation is not "testable" beyond the original correlation.

3. The "necessary but not sufficient" argument. Ryan's example of the amphibian ear is but one of a class of "key innovations" which might be termed instances of the "necessary but not sufficient" argument for the role of innovations in diversification. Other examples include the cichlid jaw apparatus (Liem 1973), gene duplications (Lauder and Liem, in press), and an increase in biomechanical complexity between the ray-finned and halecostome fishes (Lauder and Liem, in press).

The argument is usually structured as follows: evolutionary innovations are necessary but by themselves are not sufficient to account for differences in speciation or extinction rate. A new key innovation is said to create the potentiality for evolutionary change to occur along multiple morphogenetic pathways whereas others preclude such modifications. Complex structural systems are more susceptible to evolutionary change than those under strong functional/developmental constraint. If a change can increase structural complexity, it increases the chances of, and even facilitates, evolutionary differentiation. Thus, the high diversity of cichlid fishes and more advanced anurans might not have been possible without their respective innovations. As Liem (1973) and Ryan (1986) suggest, the cichlid jaw apparatus and the advanced amphibian papilla might have increased the potential for variability in feeding and vocal behavior, respectively. Schaefer and Lauder (1986:504) have expressed this argument as their "decoupling hypothesis": "a phylogenetic increase in the number of biomechanical components (as by the decoupling of primitively constrained elements) in a morphological system is related to morphological and functional diversity because of the increased possibility for change and novel connections between independent compo-
ments in a complex system. An increase in constructional flexibility is also expected to correlate with the acquisition of new functions."

How might the "necessary but not sufficient" argument be evaluated? First, the examples themselves are poorly defined as evolutionary innovations (see earlier discussion). The "amphibian papilla" and "cichlid jaw apparatus" are structural patterns seen between higher taxa, not discrete innovations postulated to have arisen at the level of differentiating populations. If, in fact, these "key innovations" arose as numerous sequential modifications ("innovations") associated with many speciation events, how might this influence our perception that these "key innovations" were necessary for subsequent diversification? Here the ontological problem of individuating a "key innovation" is critical for dissecting causation. If these features are not true evolutionary innovations arising at the population level, but are instead composites of numerous innovations, what justification do we have for ascribing a causal role to something that is not a true innovation?

Even admitting the possibility that these are true evolutionary innovations does not explain why and how the resultant variation emerged over evolutionary time in the guise of taxonomic diversity. Variation in diversity among clades of cichlids or anurans cannot be attributed to the presence of a particular jaw mechanism or inner ear structure since each is a shared synapomorphy. A single innovation does not, in general, make a species "more complex" relative to its sister species. Such complexity arises as a result of sustained diversification: characters are modifications of other characters. Without diversification, there would be no complexity to explain: complexity is an effect of diversification, not its cause. Therefore, a deterministic explanation of patterns of diversity must lie elsewhere. If a character said to be a "key innovation" cannot explain the patterns of diversity among the clades possessing it, then it must be concluded that this feature cannot also be singled out as the reason for high diversity relative to a less diverse sister group.

What about extinction rates? Can innovations influence those? Here, too, the conceptual and empirical waters are murky. Species, as cohesive en-
ities or units, do not become extinct. Species extinction is a cumulative effect of the deaths of individual organisms. Consequently, any argument that an evolutionary innovation is instrumental in influencing extinction rate must necessarily focus at the level of individual organisms and populations. How might "key innovations" such as those mentioned earlier affect the fecundity or longevity of individual organisms and thus have an indirect effect at the level of the species? Probably not at all. Another question is whether innovations present at the level of the species can be passed on to descendant species (Cracraft, in press). It is not at all clear, for example, that species have emergent properties for extinction resistance; these can generally be interpreted as an effect of the properties of individual organisms that may be manifested at higher levels. Once again, it probably will prove very difficult to erect a testable hypothesis claiming a relationship between a particular innovation and an influence on extinction rate within a clade.

In conclusion, the concept of key innovation seems to have originated from the desire to extend an adaptationist form of interpretation to hierarchical levels higher than the one at which Darwinian natural selection and adaptation operate. Thus, one can be an ardent adaptationist and still reject the utility of the concept of key innovation. The ontological, methodological, and empirical themes discussed in this chapter suggest that the concept of key innovation has little to tell us about the causal dynamics of patterns of biological diversification such as those expressed among clades.

Acknowledgments

I wish to thank Drs. Allan Larson, George V. Lauder, Robert J. Raikow, and David B. Wake for their extremely helpful and critical comments on the manuscript. This work was supported by a grant (BSR-8520005) from the National Science Foundation.
References


