

# Modularity, evolvability, and adaptive radiations: a comparison of the hemi- and holometabolous insects

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**SUMMARY** Despite recent attention given to the concept of modularity and its potential contribution to the evolvability of organisms, there has been little mention of how such a contribution may affect rates of diversification or how this would be assessed. A first key prediction is that lineages with relatively greater degrees of modularity in given traits should exhibit higher rates of diversification. Four general conditions for testing this prediction of the modular evolvability hypothesis are outlined here. The potential role of modularity as a deterministic factor in adaptive radiations is best examined by looking at historic patterns of diversification rather than just levels of extant diversity, the focus of most analyses of key innovations.

Recent developmental evidence supports the notion that phenotypes of juvenile and adult stages of insects with “complete” metamorphosis (Holometabola) are distinct developmen-

tal and evolvable modules compared to the highly correlated life stages of insects with “incomplete” metamorphosis (Hemimetabola). Family-level rates of diversification for these two groups were calculated from the fossil record. The Holometabola was found to have a significantly and characteristically higher rate of diversification compared to the less modular Hemimetabola, consistent with the idea that intrinsic differences in modularity can influence the long-term evolvability of organisms.

The modular evolvability hypothesis also makes a second key prediction: that characters in more modular clades will exhibit greater levels of variation due to their independence. This provides an independent, phenotypically based test of the hypothesis. We discuss here how this second prediction may be tested in the case of the Hemi- and Holometabola.

## INTRODUCTION

The evolvability of an organism is its intrinsic capacity for evolutionary change (Wagner 1996; Gerhart and Kirschner 1997; West-Eberhard 1998). It is a function of the range of phenotypic variation the genetic and developmental architecture of the organism can generate, and thus the amount of variation available on which selection can act. A number of characteristics of organismal organization are thought to contribute to evolvability (Conrad 1990; Gerhart and Kirschner 1997). These characteristics reduce genetic or developmental linkages that may act to constrain the production of adaptive phenotypic variation, or in other words, minimize “developmental constraints” (Alberch 1982; Cheverud 1984; Maynard Smith et al. 1985; Lande 1986, von Dassow and Munro 1999).

The most fundamental of these organizational characteristics is a degree of independence between different aspects of phenotype such that individual characters are able to evolve in response to selection with little or no associated, and possibly detrimental, effects on other characters. This characteristic has been described in various ways, including “quasi-independence” (Lewontin 1978), “compartmentation” (Kirschner and Gerhart 1998), and “modularity” (Raff 1996; Wagner and Alt-

enberg 1996; Nagy 1998; Brandon 1999; von Dassow and Munro 1999; Raff and Raff 2000). “Modularity” therefore describes both a low level of linkage between the developmental processes that give rise to different phenotypic characters, as well as a high level of integration within processes such that a distinct entity called a “module” is identifiable.

A number of studies have described how certain developmental processes and the morphologies they produce have likely evolved within or across certain taxa (reviewed by von Dassow and Munro 1999). These studies provide some of the best examples of how modular design in animal form may have contributed to certain transformations; insofar as these developmental mechanisms and their corresponding morphologies have evolved, they can be considered cases of evolvability. The next step in exploring the role of modules in evolvability, however, is to not only describe the link between evolutionary change in development and phenotype but also to generate hypotheses that can test what the long-term consequences of modularity have been to the evolvability taxa in a phylogenetic context.

A simple prediction is that lineages made up of organisms with relatively greater degrees of modularity should, over the long term, exhibit greater levels of taxonomic diversity

than less modular lineages (Gerhart and Kirschner 1997). Here, I briefly discuss some of the key conceptual and methodological considerations that must first be met before diversity between clades can be used as a basis for testing modular evolvability; then, I summarize them in the form of four general conditions. As an example of how these conditions may be applied in practice, I compare the holometabolous and hemimetabolous insects, which exhibit qualitatively different degrees of life-stage modularity due to their different types of metamorphosis (commonly known as “complete” and “incomplete,” respectively). I show here that the Holometabola have displayed a characteristically greater rate of family-level diversification throughout 250 of their 300-million-year history, which has resulted in their present taxonomic success compared to the Hemimetabola. This observation is consistent with the hypothesis that modularity can influence the long-term evolvability and diversification of organisms.

### **Conceptual issues and the four conditions necessary for testing modular evolvability**

#### ***Identification of modules and their role as key innovations in adaptive radiation***

If greater modularity does in fact confer greater evolvability, this should become manifest in the form of radiations of diversity relative to less modular clades. As in other analyses of adaptive radiations, the best types of comparisons are those between sister taxa where one lineage exhibits a “key innovation” that is absent in the sister lineage (Mitter et al. 1988; Brooks and McLennan 1993; Guyer and Slowinski 1993; Wiegmann et al. 1993a). A greater degree of modularity can be considered a key innovation since it is a characteristic that a taxon possesses, enabling it to differentially diversify relative to other clades. However, unlike many postulated key innovations, modularity is not identifiable with any one phenotypic character, but rather with the overall ability to produce variation in morphological structures that can function as adaptations to novel environments.

In this way, the key innovation of greater modularity is not a phenotypic character per se, but rather a property of those characters. Because of this, testing a hypothesis of modular evolvability is not concerned with how the presence or absence of a single phenotypic character in lineages correlates to their relative taxonomic diversity (as for traditional key innovations), but instead how differences in the ability of characters to evolve independently of each other is associated with diversification within a lineage.

Comparing differences in modularity between lineages involves the identification of a module as an entity that comprises two components: the phenotypic characters on which selection acts, and the underlying developmental processes that form the character or sets of characters where potential

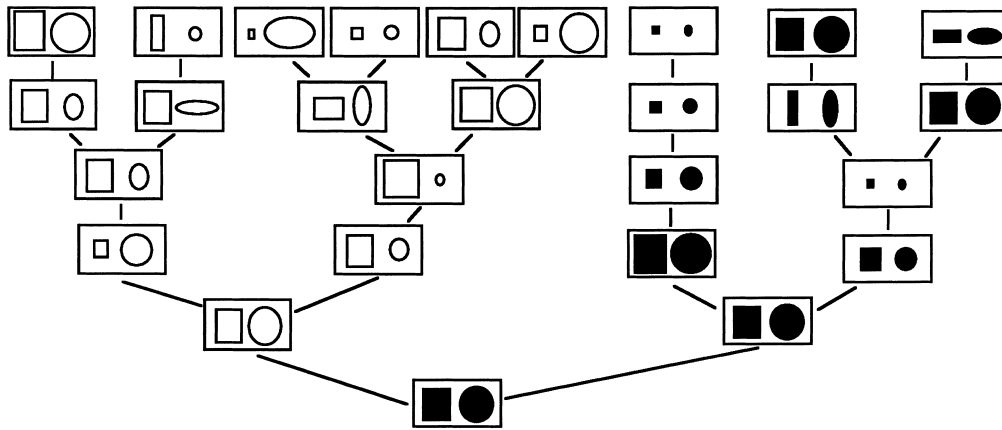
constraining linkages may operate. Brandon (1999) has described such an entity as a “module of selection.” However, the term “evolvable module” may be more apt for describing an entity that can both be acted upon by selection, as well as respond to it. This also distinguishes it from the term “developmental module,” which is commonly used to describe processes and pathways that are conserved throughout development, but which do not necessarily correspond to an identifiable phenotypic character (Raff 1996; Kirschner and Gerhart 1998; Nagy 1998; Raff and Raff 2000).

In principle, circumscribing an evolvable module only requires that phenotypic characters be linked to a process within the developmental hierarchy that is discernibly dissociable from other developmental processes at that level. Since the primary goal of this article is to address how modular evolvability can be applied in a historical framework, a more thorough discussion of the various challenges involved in module identification is beyond the scope of what is addressed here. For this, I refer the reader to comprehensive treatments of this topic provided by von Dassow and Munro (1999), Raff and Sly (2000), and Raff and Raff (2000). It is clear, however, that the details and justification of evolvable module circumscription will depend greatly on the organisms, characters of interest, and specific questions being asked within a given study. For example, while a wing disk may be a suitable evolvable module for examining the evolution of wing morphology compared to other appendages in *Drosophila*, the *Distal-less* signaling pathway may not be, since it takes part in the formation of all appendages. Such considerations will apply equally to “spatial modules,” where the phenotypes and developmental mechanisms being compared are expressed concurrently in the organism, as well as to “temporal modules,” where the evolvable modules of interest are manifest at different times in ontogeny, such as metamorphic stages.

#### ***Module stability and the comparison of appropriate taxa***

Ideally, we will want to compare sister taxa like those shown in Figure 1 that possess different degrees of modularity or different numbers of evolvable modules with respect to certain phenotypic characters. Although the attributes of these characters may evolve over time (independently in the white clade and correlated in the black clade), the degree of modularity between these characters remains stable throughout their respective lineages.

As is the case with all comparisons of adaptive radiation, care must be taken to assure that suitable (sister) taxa are actually being compared and that the timing of origination of the key innovation (be it modularity or a specific phenotypic character) is known. This is of particular concern if (1) the “innovation” is evolving quickly in lineages, indicated by high levels of homoplasy (Fig. 2A) or (2) if extinction has been common, and therefore substantial amounts of data re-



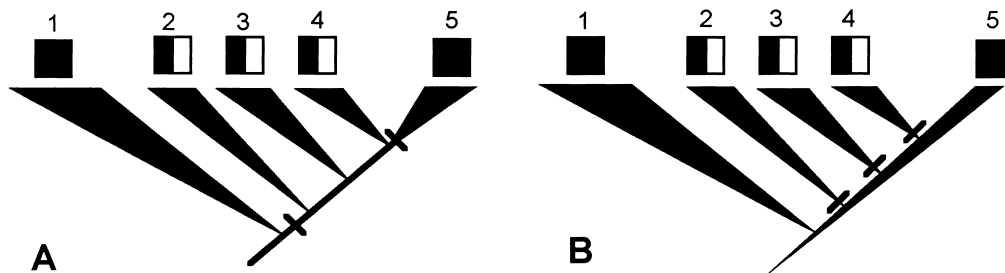
**Fig. 1.** Hypothetical example in which testing the role of modularity in evolvability and diversification is clear-cut: modular and non-modular clades are sister taxa and the state of modularity between characters is stable throughout their respective histories. Boxes represent taxa; squares and circles represent phenotypic characters that the taxa possess. Characters that are white are modular (independent of each other developmentally), whereas black characters are linked to each other. This is reflected in the various ways the sizes and shapes of the square and circle characters may vary in the modular clade (white) compared to the non-modular case (black), where the evolution of size and/or shape is correlated between characters.

garding the evolution of the clade and its modularity are missing (Fig. 2B).

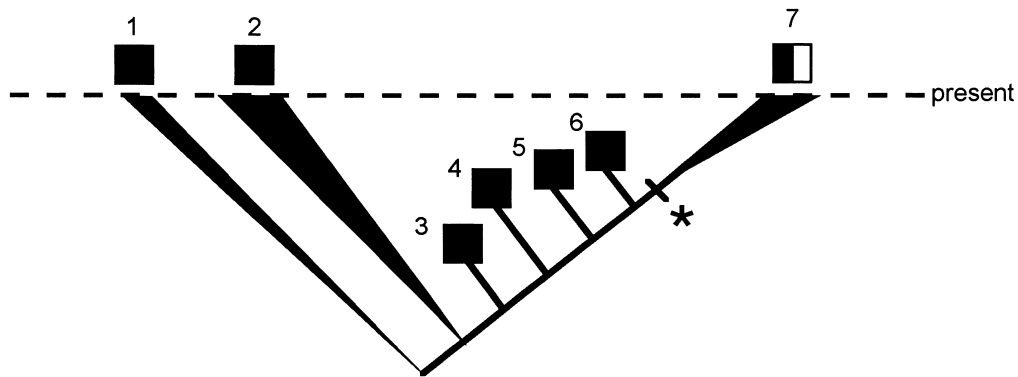
Accurately determining where within a clade a key innovation originated, and therefore which taxa are appropriate to compare, does not usually pose much difficulty. This is because traditional key innovations, such as a discrete morphology or behavior, arise only once or relatively infrequently in a lineage (but see Hunter and Jernvall 1995). The origin of modularity, however, is much more elusive. As an inherent organizational property, modularity between phenotypic characters is by definition ever-present in the history of organisms. More significantly, the relative degree of modularity between characters inevitably and continuously changes over macroevolutionary time as patterns of natural selection change and

the developmental architecture of organisms evolve. New evolvable modules will arise and others disappear. Some may appear either *de novo*, resulting from the integration of previously independent modules due to the selection for correlations (developmental linkage) between characters to form adaptive complexes (Cheverud 1996), or through the division of previous modules into new independent units (Wagner and Altenberg 1996). This means that one must be careful in assuming that the association between a given phenotypic character and an underlying developmental mechanism is truly stable throughout their histories (von Dassow and Munro 1999).

Two primary means exist for trying to determine the timing and nature of changes in modularity within a lineage so



**Fig. 2A.** Solid boxes represent taxa with correlated (non-modular) characters; split boxes represent taxa with independent (modular) characters. Modularity is evolving quickly in the clade, resulting in homoplasy. With only phylogenetic information from extant taxa, it may often be difficult to unequivocally determine at what points modularity changed in a clade and therefore which taxa are appropriate to compare. For example, if the history of modularity in the phylogeny is interpreted as in (A), then clades 4 and 5 are sister taxa of the same age, and a comparison of their standing taxonomic diversities reliably estimates their relative rates of diversification. If, however, the modularity in 2, 3, and 4 are independent events as in (B) (one less parsimonious step), rates of diversification cannot be estimated simply from extant diversity since comparable sister groups are not present. Instead, rates of diversification must be calculated for each clade individually and then compared.



**Fig. 2B.** With only knowledge of the extant taxa, it may appear that clade 7 gained modularity (split-box) upon diverging with clade 2 when in actuality clade 7 has only been modular since its divergence from clade 6. This may lead to the inappropriate comparison of clade 7 and clade 2 and the conclusion that modularity of these characters has not influenced their relative rates of diversification. In this case, their standing taxonomic diversities are not a reliable estimate of their respective rates of diversification since modularity has a much more recent origin in clade 7 than phylogeny based on extant taxa alone may suggest.

that sister taxa diversification can be compared over time spans where evolvable modules are stable, as in Figure 1. One approach is the use of developmental data from extant taxa compared in the context of their phylogenetic relationships, a method that has been widely applied in the analysis of character evolution and adaptive radiation (Lauder and Liem 1989; Brooks and McLennan 1993; McKittrick 1993). However, caution is needed when relying solely on developmental data and phylogenies based on extant taxa to determine how and when modularity changed and which groups are appropriate to compare. As mentioned before, this is particularly the case if modularity of the characters is suspected to have evolved quickly or if extinction has been common in the lineages in question (Figs. 2A and 2B).

Another approach is the use of fossil data, which provides information for identifying evolvable modules and their changes through time not afforded by extant taxa. For example, if the fossil record contains multiple samples per unit time period, the absence or presence or correlation of phenotypic characters relative to each other can provide a means to assess the degree of developmental linkage between them. Strong morphometric correlations, or lack thereof, among characters can be used to infer the nature of underlying developmental processes and can act as a proxy for determining evolvable modules in fossil specimens. Ideally, both phylogenetic and developmental data from extant taxa and fossil data would be used in concert whenever possible.

#### **Identifying biologically, ecologically, and historically comparable taxa**

Modularity is of course only one of a number of factors, both intrinsic and extrinsic, that can influence the relative rates of diversification (Mitter et al. 1988; Raikow 1988). It is therefore important to study taxa in which confounding factors

are minimized so that any differences in diversification may be confidently ascribed to differences in modularity.

We expect differences in modularity between lineages to produce consistent differences in their “intrinsic rates” of diversification; that is, they should exhibit stable and characteristic rates of diversification, analogous to the net reproductive rate constant, “ $R_0$ ,” used in models of population growth (Sepkoski 1996). To minimize the possible effects of other intrinsic biological factors that can influence the rates of diversification, we will want to choose clades that are similar to each other in life history traits such as generation time, reproductive mode, or dispersal ability. To minimize the equally powerful role of extrinsic factors, care should be taken to choose phenotypic characters that, while they differ in degree of modularity, do not differ radically between lineages in their functional (and thus adaptive) contributions to fitness. That is to say, no other major “key innovation” other than the origination of modularity itself should differ between the sister taxa. Likewise, the taxa chosen should have experienced similar macroecological and biogeographical histories, and hence have had comparable opportunities to evolve through exposure to new niches or extinction events over a given time span.

#### **Testing adaptive radiations by the pattern of diversification**

If sister taxa are found in which all intrinsic and extrinsic factors, except for the modularity of the characters in question, are comparable, then consistently different long-term trends in diversification rates between them may indicate a deterministic role for modularity. However, rather than comparing patterns of diversification for consistent long-term trends, many analyses of adaptive radiation have relied solely on comparing extant levels of diversity between sister taxa. In principle, this provides an estimate of diversification rate by

dividing this taxonomic diversity by the time since the origination of the clade. However, this method lacks information on the temporal pattern of diversification and whether it has exhibited steady and characteristic branching consistent with an intrinsic property like modularity. Analyzing patterns of diversification in any reliable way requires having knowledge of the taxonomic diversity throughout the history of the clade, something that a single measure (extant diversity) cannot provide.

Examinations of adaptive radiation relying solely on standing taxonomic diversity have faced two major and closely related problems. The first has been that of circularity, since the initial observation of differential diversity that spawns a hypothesis of adaptive radiation is also the basis by which that hypothesis would be tested (Guyer and Slowinski 1991, 1993). A number of null models have been developed that allow one to test whether cases of differential diversity are significantly different from random expectation (Raup et al. 1973; Dial and Marzluff 1989; Slowinski and Guyer 1989; Guyer and Slowinski 1991). However, subsequent attempts to explain such diversifications by invoking particular key innovations have raised the second problem of how such deterministic hypotheses can be sufficiently tested (Raikow 1986, 1988; Lauder and Liem 1989; Guyer and Slowinski 1993). To overcome the speculative “just so” nature of such explanations, it has been argued that the analysis of multiple, independent taxa in which the postulated innovation has arisen provides a more objective and statistical means of assessing the link between these innovations and diversification (Raikow 1988; Mitter et al. 1988; Guyer and Slowinski 1993). Nevertheless, such analyses still depend on the very basis on which the original hypotheses were generated, namely standing taxonomic diversity. Analyzing patterns of diversification throughout the history of a clade for characteristic and statistically significant trends, in contrast, provides a means to assess the deterministic role of evolvability in diversification, independent of extant taxonomic diversity, and therefore overcomes the problem of circularity as well as the need for multiple, independent examples of the innovation.

Determining patterns of diversification has traditionally meant relying on a substantial fossil record, which potentially limits the taxa that can be compared by this method. In an attempt to get around this obstacle, sophisticated methods of phylogeny reconstruction and rate estimation are being developed that allow both the rates and patterns of diversification to be inferred from molecular data alone (Sanderson and Donoghue 1994; Zink and Slowinski 1995; Paradis 1997, 1998). While such “tree-based” methods may provide a means to broaden the taxa in which diversification rates can be determined, they are still in their infancy and depend on various assumptions regarding the rates at which the focal genes evolve (Sanderson and Donoghue 1996), including the

basic assumption that the rate of gene evolution is representative of the species that contain them. More significantly, molecularly derived diversification rates and their models cannot provide key information regarding extinct taxa nor distinguish between increased speciation versus decreased extinction as the cause for differential diversification between taxa (Zink and Slowinski 1995; Paradis 1998). For these reasons, although restrictive, a fossil record may still provide the most reliable and informative means by which to assess patterns between clades and to determine whether they exhibit distinct intrinsic rates of diversification that are predicted by the modular evolvability hypothesis.

We can conclude, then, that in order to assess whether modularity has contributed to differential diversification between sister taxa, four general conditions must be met: (1) The taxa must possess identifiable evolvable modules (i.e., phenotypic characters of adaptive interest, which appear to be determined by underlying developmental processes that are modular); (2) The number of evolvable modules should clearly differ between the sister taxa, and this number must remain stable within each taxon throughout the time span being considered; (3) The clades should be similar in general life history and ecology so that possibly confounding intrinsic and extrinsic factors that affect diversification are minimized. In particular, the phenotypic characters in question should have experienced relatively similar selective environments and thus equivalent ecological opportunities to diversify over the long-term; (4) Sufficient, and ideally fossil, data should exist for the taxa so that long-term rates and patterns of diversification can be compared for the influence of an intrinsic biological factor, like modularity.

### **The diversification of the hemi- versus holometabolous insects: an example of modular evolvability?**

To illustrate how the above conditions might be applied to actual taxa, I will compare the hemi- and holometabolous insects. This case serves as a putative example of a group in which metamorphic life-stage modularity has contributed to differential evolvability and diversification.

#### ***Meeting the first three conditions***

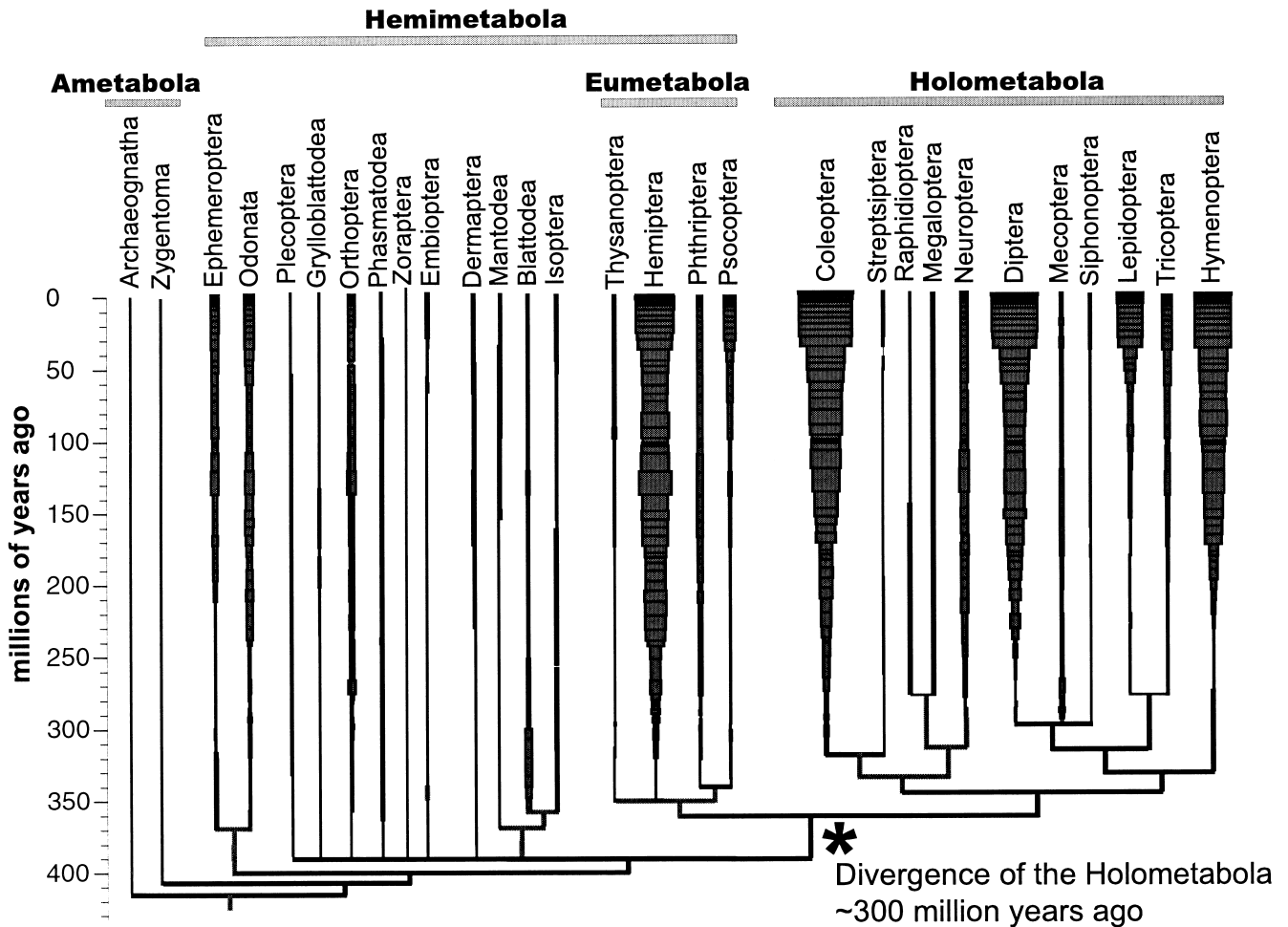
Insects are the most successful macroscopic group in terms of taxonomic diversity and provide an excellent example of where modularity has likely played a significant role in differential diversification and adaptive radiation. Since their origination from arthropod ancestors over 400 Mya, the insects have undergone radical evolution in their development such that three types of metamorphosis have emerged. These include: (1) the wingless Ametabola (Apytergota), which develop directly and whose juvenile and adult stages are marked only by differences in size and sexual maturity; (2) the Hemimetabola (Exopytergota) with a metamorphic trans-

formation between juvenile and adult forms involving primarily the maturation of genitalia and the externally developing functional wings; and (3) the Holometabola (Endopterygota), in which extensive morphological remodeling of juvenile structures occur, resulting in adults with a phenotype that is quite different from that of larvae. These three broad forms of metamorphosis are called “simple,” “incomplete,” and “complete” metamorphosis, respectively, and represent an evolving sequence from the primitive ametabolous to hemimetabolous to the most derived holometabolous type of development.

The Holometabola is widely accepted as a monophyletic group, originating from hemimetabolous ancestors during the Permian 300 Mya (Labandeira and Phillips 1996; Kristensen 1999); its direct hemimetabolous sister group is the “Eumetabola” (Sehnal et al. 1996) (see Fig. 3). The taxo-

nomous success of the insects is largely owed to members of the Holometabola, which constitute 80–90% of all extant species in the class. The immense radiation and eight-fold higher diversity of the Holometabola over the Hemimetabola has often been attributed to the advent of its “complete” metamorphosis, which is thought to allow the divergent evolution of stage-specific morphological and life-history specializations in juveniles and adults (Kukalova-Peck 1991; Truman and Riddiford 1999; Gullan and Cranston 2000). This argument is essentially a hypothesis of greater modular evolvability of the Holometabola relative to the Hemimetabola, whose less drastic, nonpupal metamorphosis does not enable the same developmental, and thus phenotypic, dissociation between life stages.

To what extent do the juvenile and adult stages of insects, and metamorphic life stages in general, qualify as evolvable



**Fig. 3.** Phylogeny of the insects, with the three major developmental types: the Ametabola, Hemimetabola, and Holometabola. The Hemimetabola is a paraphyletic group; however, the hemimetabolous Eumetabola and Holometabola appear to be monophyletic sister taxa. The numbers of families in each order through macroevolutionary time, up to the Holocene but not including extant diversity, are represented by the width of the boxes. Extinct lineages are omitted for clarity. Branching adapted from Kristensen 1991; Labandeira 1998.

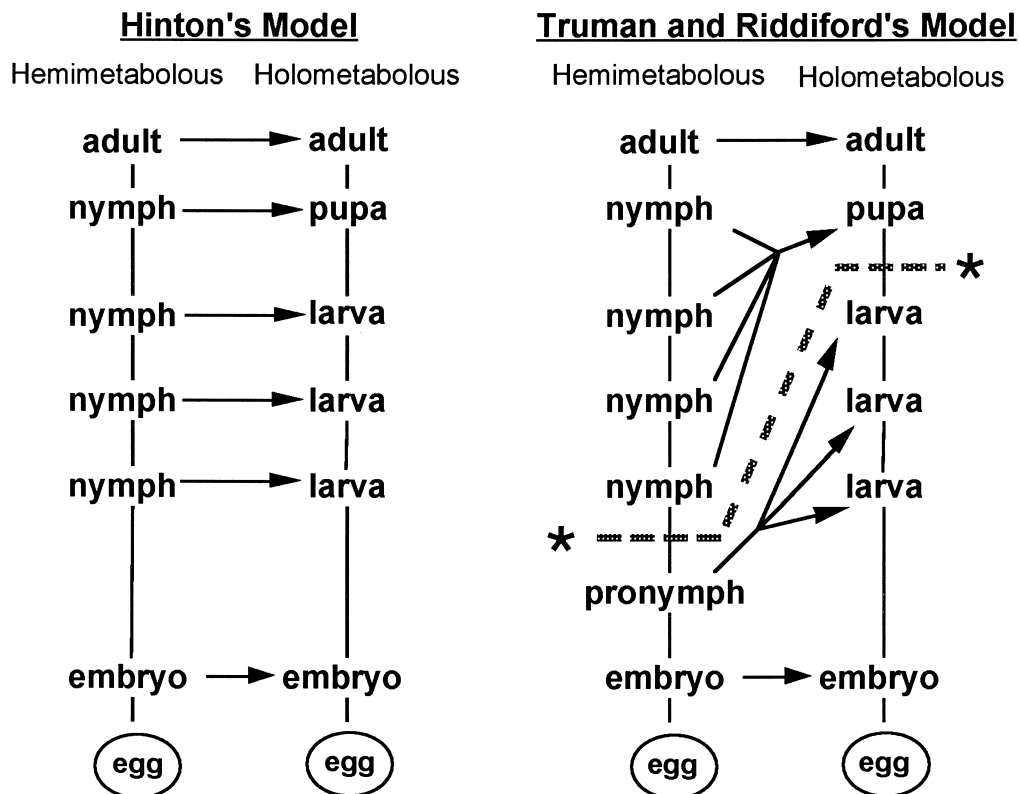
modules in (1) existing as adaptively significant phenotypic characters, and (2) being created by underlying modular developmental processes? A large body of both theoretical and empirical observations supports the idea that the various morphologies and behaviors characteristic of discrete life stages of metamorphic organisms are adaptive for a number of reasons (for comprehensive review see Ebenman 1992; Moran 1994). These include size-dependent resource utilization (Werner 1988); maximization of population growth through minimization of intraspecific conflict between life stages (Ebenman 1987); and structural specialization for different tasks at different stages in their ontogeny (Bryant 1969), such as mouthparts for the exploitation of radically different food sources (Labandeira 1997).

Recent work by Truman and Riddiford (1999) supports the notion that the juvenile and adult stages of the Holometabola truly represent qualitatively different degrees of developmental modularity than the equivalent stages of the Hemimetabola. Their developmental data provide the most conclusive evidence to date on longstanding controversy regarding the origin of holometabolous metamorphosis and its

pupal stage (Berlese 1913; Poyarkoff 1914; Imms 1938; Hinton 1948; Helsop-Harrison 1958).

Truman and Riddiford contradict the most widely accepted model, that of Hinton (1948, 1963, 1976), which contends that the pupal stage of Holometabola is essentially a radicalized last instar of a hemimetabolous juvenile and, therefore, that the juvenile and adult stages of the Hemi- and Holometabola are homologous. Hinton's model implies that the difference between metamorphic types, though significant, is fundamentally continuous in nature. In contrast, Truman and Riddiford's endocrinological and morphological analysis of the two groups suggests that the juvenile stage of the Holometabola is in fact homologous to a largely unexpressed pre-juvenile stage called the "pronymph" in the Hemimetabola, not its "nymphal" juvenile stages. The nymphal stages of the Hemimetabola instead appear to have been contracted in the Holometabola to form its pupal stage (Fig. 4).

According to the Truman-Riddiford model, the transition from pronymph to nymph coincides with a fundamental developmental switch-point when the development of embryonic tissues ends, and differentiation and growth of primor-



**Fig. 4.** How life stages between the hemimetabolous and holometabolous insects correspond according to the Truman and Riddiford's (1999) theory of the evolution of metamorphosis. According to this model, the juvenile stages of hemimetabolous insects (nymphs) are not homologous to that of the juvenile stages in holometabolous insects (larvae), but rather arose from another developmental stage called the "pronymph." The starred, dashed line shows the critical pronymphal→nymphal developmental transition and how it has shifted in evolution.

dia that form adult structures begins. In the Hemimetabola the pronymphal→nymphal transition occurs at egg hatching and results in a nymphal juvenile stage and adult stage whose phenotypes are remarkably similar. A heterochronic shift of this developmental transition to the pupal stage in the Holometabola has resulted in juvenile and adult stages whose phenotypes are fundamentally more developmentally dissociated, and thus evolvable, in comparison. In effect then, a developmental stage lacking a clear ecological role in regards to the external environment—the pronymph of the Hemimetabola—was transformed into a novel life history stage in the larvae of the Holometabola.

If we accept (1) the adaptive significance of different metamorphic life stages, and (2) the developmental evidence that holometabolous juvenile and adult stages represent two modules relative to the single module these stages comprise in hemimetabolous insects, then the first two conditions for testing a hypothesis of evolvable modularity have been met. This includes the stability in the number and identity of evolvable modules within the sister taxa mentioned in condition two. Although there are superficially “pupal-like” larval stages in whiteflies (Family: Aleyrodidae) and thrips (Order: Thysanoptera) of the Hemimetabola, true holometabolous metamorphosis appears to have evolved only once and has persisted with no reversals to hemimetabolism (Fig. 3).

The third condition, comparing sister taxa that have experienced generally comparable intrinsic and extrinsic factors, can also be met in the Hemi- and Holometabola. Because of the antiquity and geographic ubiquity of insects at the Hemi- and Holometabola level of comparison, we have a unique situation where the common selective environment of relevance in this case is the earth itself over the last 300 million years. Likewise, at this level, neither the Hemi- nor Holometabola as a whole possess any single trait (i.e. key innovation), besides differing metamorphoses, which might confound their comparison from an ecological or life history perspective.

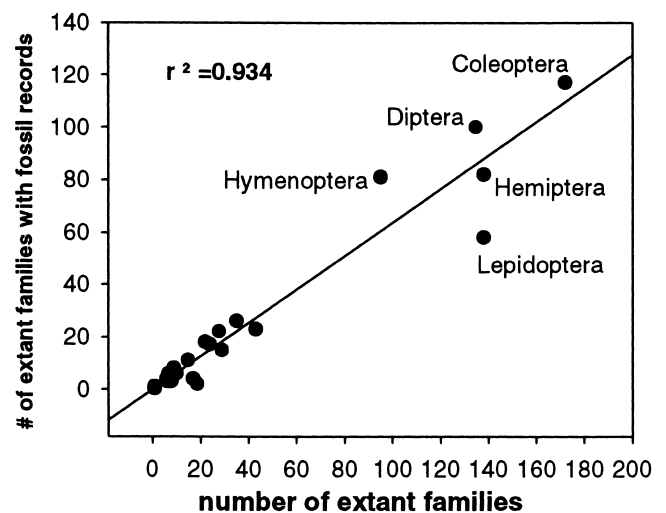
While meeting the third condition in this case is made easy by comparing such large taxonomic groups, taxa within both the Hemi- and Holometabola possess a wide variety of trophic and life history habits, and differences in such traits are known to significantly influence diversification between sister taxa. Examples of this include phytophagy versus non-phytophagy (Mitter et al. 1988), parasitism versus predation (Wiegmann et al. 1993a), and gymnosperm versus angiosperm feeding (Farrell 1998). Restricting clade comparisons on the basis of trophic or life history habits may therefore be necessary to properly test modular evolvability at lower taxonomic levels. At the broad Hemi- and Holometabola level of comparison, however, the relative diversity of habits that members of both groups have evolved is part of the data needed to assess modular evolvability, rather than a potentially confounding factor. In the last section, I will come

back to this point and discuss how the diversity in phenotypes between the evolvable modules of life stages provides an additional means to test the modular evolvability hypothesis.

#### **Condition four: the fossil record of the Hemi- and Holometabola and their rates of diversification**

Given the above framework, we are now ready to address the question of whether the temporal patterns and magnitude of differences in diversification between the Hemi- and Holometabola support modular evolvability as a contributing factor. The necessary data on long-term rates of diversification in condition four were generated from a compendium compiled by Labandeira (1994), which lists the presence of insect families, including first and last appearances, throughout the geologic record.

Family-level data are very suitable for addressing the question at hand. Within the fossil record, insect families are less likely to suffer from inconsistent sampling or ambiguous taxonomy than analyses at lower taxonomic levels. Also, insect families often differ discretely in their trophic habits and associated morphologies (Labandeira and Sepkoski 1993). This makes family-level diversity a reasonable proxy for phenotypic diversity in lieu of specific morphological and behavioral data in this group. Insects are sufficiently diverse at this taxonomic level to provide an ample number of data points from which trends can be determined with some confidence. Figure 5 illustrates that diversity in the fossil record



**Fig. 5.** The relationship between the number of extant families with fossil records versus the total number of extant families in the various hemi- and holometabolous orders. The regression shows that there is no particular bias across orders with different degrees of extant diversity in terms of their fossil representation. The possible exception is the Lepidoptera (butterflies and moths). Major orders from each group are labeled.



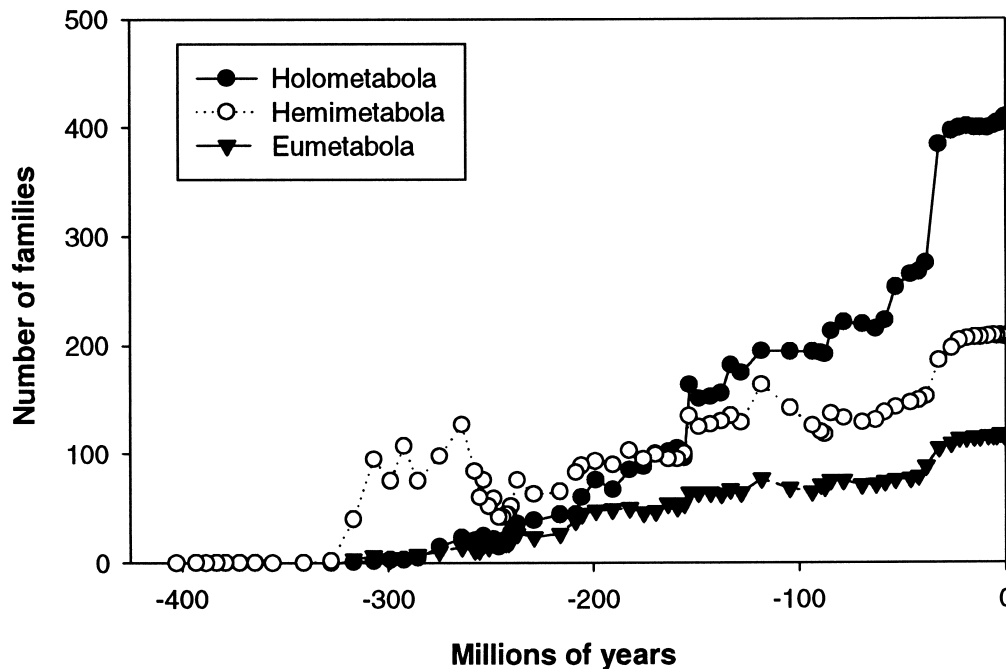
corresponds extremely well with extant diversity. No sampling bias is apparent across orders based on their relative sizes. The only order that appears to be underrepresented is the Lepidoptera (butterflies and moths) (Labandeira and Sepkoski 1993).

From Figure 3, we see that only a portion of the Hemimetabola, the Eumetabola, are actually sister taxa to the Holometabola, with the rest of the hemimetabolous orders being paraphyletic. Whereas the relevant comparison of diversification will therefore be between the Eu- and Holometabola, contrasting the Holometabola to the Hemimetabola as a whole is useful for illustrating overall diversity trends of these two developmental types. For example, trends in family-level diversity over time clearly demonstrate that the Holometabola have diversified more than all of the Hemimetabola during the last 150 My (Fig. 6A).

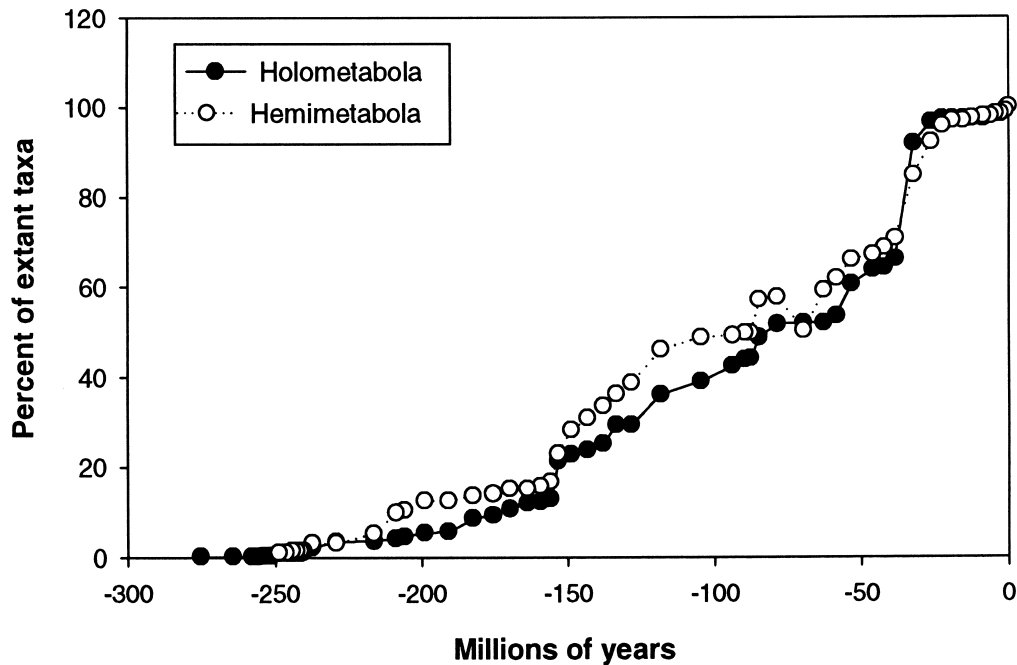
However, differential extinction can affect differences in net diversity over time just as much as differential diversification. Lyellian survivorship curves show what proportion of taxa present at given time intervals in the past are still present today, and are useful in assessing relative rates of extinction in groups with low overall levels of extinction, such as insects (Gilinsky 1991; German 1991; Labandeira and Sepkoski 1993). The Lyellian survivorship curves of these two groups are very similar (Fig. 6B). The rates of extinction for the Hemi- and Holometabola were calculated in approximately 6 to 20 My intervals throughout their shared history.

These intervals represent groupings of three consecutive geologic stages that were used to average out the effects of sampling error sometimes occurring within a single geological stage (e.g., no fossil record in a given stage but multiple records in those that precede and follow it). We find there is no significant difference between the overall extinction rates of the two groups (paired *t*-Test,  $p = 0.94$ , two-tailed). Thus, differential extinction in the Hemimetabola cannot explain the greater taxonomic diversity of the Holometabola.

If we now look at rates of diversification and make the comparison between the Holometabola and its sister group, the Eumetabola, the differences in family-level diversification between the two metamorphic types is even more pronounced (Fig. 6A). Normalized rates of family-level diversification for ~6 to 20 My intervals were calculated for both groups from a time soon after their divergence (Fig. 7A). While the rates of diversification show considerable heterogeneity over time, the Eu- and Holometabola trends track each other remarkably well. This highly parallel pattern of diversification is exactly what is expected if the two groups have experienced equivalent selective environments and macroecological histories, as earlier argued. With potential confounding extrinsic influences thus factored out, differences in rates of diversification should reflect the influence of modularity. The pair-wise differences of these two graphs in Figure 7B, illustrate a highly significant difference between the two groups: the Holometabola exhibit a systemat-



**Fig. 6A.** The number of fossil families within the hemi- and holometabolous insects over macroevolutionary time. Several hemimetabolous orders went extinct at the end of the Permian, 250 Mya. Since the end of the Jurassic, approximately 150 Mya, the holometabolous insects have been dominant in family-level diversity, and even more so in species-level diversity.



**Fig. 6B.** Lyellian survivorship curves for families of the Hemi- and Holometabola. Points at a given time represent the percentage of taxa that have persisted to the present. The steeper the decay of the curve, the greater the rate of extinction in that group. The Hemi- and Holometabola have almost identical curves, suggesting their rates of extinction are similar, and therefore differential diversification, not extinction, has been responsible for the relative taxonomic success of the Holometabola.

ically greater intrinsic rate of diversification per time interval than the Eumetabola over most of their evolutionary history (paired *t*-Test,  $p = 0.004$ , one-tailed).

## DISCUSSION

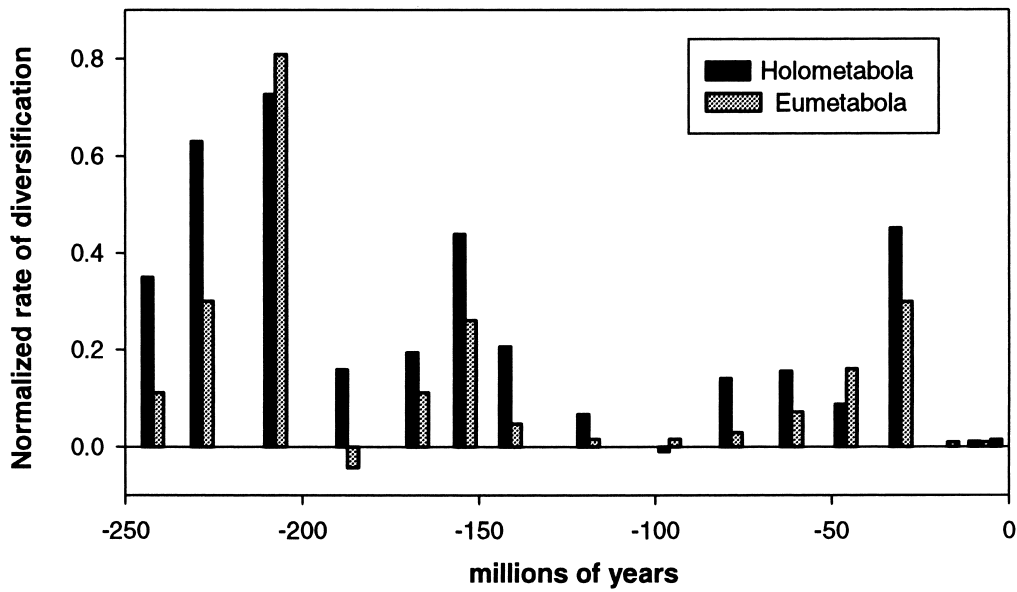
### Phenotypic diversity and the second prediction

Greater modularity between juvenile and adult life stages in the Holometabola is presumed to increase the ability of the stage phenotypes to evolve independently and result in higher rates of diversification than are possible in the Hemimetabola. This prediction is supported by the comparison of long-term diversification patterns of the two groups presented here. A possible criticism of using comparisons of diversification patterns to test a hypothesis of modular evolvability is that it largely depends on negative evidence, insofar as modularity as an underlying agent can be invoked only after we believe the effects of “all” other confounding extrinsic and intrinsic factors have been discounted.

However, the modular evolvability hypothesis differs from other tests of adaptive radiation by providing a second key prediction: that a correspondingly greater variety in phenotypes is expected between the characters in question in the more modular clade. For example, not only would we predict that the Holometabola should show a greater intrinsic rate of

diversification relative to the less modular Hemimetabola, but we also expect to see greater variety in the combinations of juvenile and adult stage phenotypes present per unit of taxonomic diversity in the Holometabola (as illustrated in Fig. 1). In this way, a hypothesis of modular evolvability provides an independent means for testing the role of an innovation based on phenotypic, rather than taxonomic, diversity. Lauder and Liem (1989) proposed a similar morphologically based method to assess the role of historical factors, such as the duplication of genes or structural elements in diversification. This is, in essence, a form of the modular evolvability hypothesis because it argues that, “Clades possessing, as a novelty, a greater number of independent (decoupled) structural or functional components of design will exhibit an increase in morphological and functional diversity when compared to sister clades with fewer independent design elements” (Lauder and Liem 1989).

Comparisons of the general morphology exhibited between life stages in the Hemi- and Holometabola appear to provide qualitative support for this phenotypic diversity prediction. For example, detailed studies on mouthparts, one of the most significant life-history characters in insects, show that holometabolous insects possess a more diverse array of mouthpart types (23), compared to that found within the whole of the Hemimetabola (11) (Labandeira 1997). This morphological diversity in the Holometabola seems to corre-

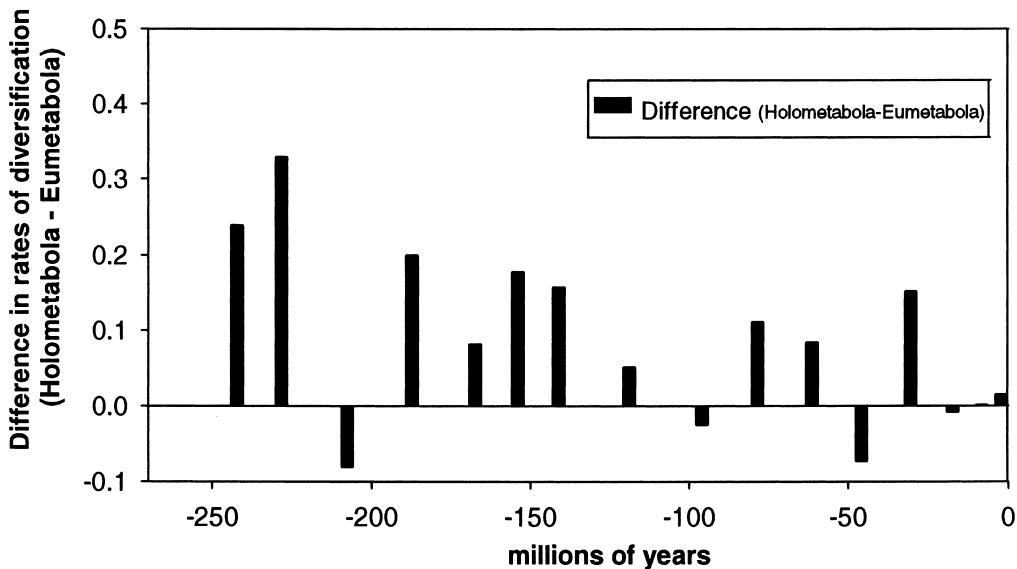


**Fig. 7A.** Normalized rates of diversification, (# of families at end / # of families at beginning of an interval)–1, for approximately 6–20 My intervals for the Eumetabola and the Holometabola. Although there is considerable variation in the diversification rates through time, the rates of both groups appear to follow the same overall trend.

late well with functional diversity. The largest Hemimetabolous order, the Hemiptera, contains only two functional feeding types on vascular plants (piercing-and-sucking and spore/pollen feeding), whereas the four dominant orders of the Holometabola (Coleoptera, Lepidoptera, Diptera and Hymenoptera) each contain between five and six functional feeding types. Like the morphological diversity, much of this functional diversity in the Holometabola can be attributed to

the fact that feeding strategies often differ between their juvenile and adult stages (Labandeira, 1998).

Still, extensively testing the phenotypic diversity prediction in the two groups, in a quantitatively rigorous manner, presents a formidable task because of the vast numbers of taxa involved as well as a dearth of the necessary information on life-stage traits for many species. In principle, indices can be developed to quantify the disparity in morphology,



**Fig. 7B.** The normalized rate of diversification of the Holometabola minus that of the Hemimetabola. The overall positive values indicate the Holometabola have had characteristically higher rates of diversification compared to their hemimetabolous sister group, the Eumetabola, over macroevolutionary time (paired *t*-Test, *p* = 0.004, one-sided).

behavior, habitat, and a number of other traits between life stages in taxa. This information, together with phylogenetic analyses of the number of times that character combinations have changed throughout the history of clades, can be used to test the second prediction and thus provide a more rigorous test for the role of modular evolvability in the diversification of the Holometabola.

### Alternative hypotheses and finer grades of metamorphosis

Different orders within the Hemi- and Holometabola display a great range in family-level diversity. Some of this may be attributable to unresolved taxonomic issues among ordinal classification in the insects. For example, the number of orders reported to comprise the two groups ranges considerably among different textbooks, with 15 to 18 orders in the Hemimetabola, and 9 to 11 orders in the Holometabola (Evans 1984; Brusca and Brusca 1990; Borror et al. 1992; Romoser and Stoffolano 1994). Further, the most dominant order of the Hemimetabola, the Hemiptera (considered here as one order), is often broken into two separate orders of roughly equal size.

However, the concentration of diversity in particular holometabolous orders, such as the Coleoptera, Diptera, Lepidoptera, and Hymenoptera (see Fig. 3) has led many authors to conclude that key innovations specific to those orders have been responsible for their success (Gilliot 1995; Kristensen 1999). The apparent success of the Holometabola as a whole, it might then be argued, is not a product of one group-wide trait such as life-stage modularity, but rather a coincidental artifact of possessing four peculiarly diverse orders whose sizes are due to innovations unique to each of them.

Whereas it may be difficult to distinguish between these two hypotheses, it should be obvious that such variation in diversity between orders would be expected in the case of modular evolvability. Although modularity may play a primary role in diversification by providing the potential for evolvability, forces and historical factors—such as selection, chance extinction, or biogeography—play key roles in patterning this diversity at these lower, ordinal levels. Because of this, not all taxa will have the opportunity to “make use” of the advantage evolvability offers. Rather, the expectation is that on average a greater proportion of taxa (in this case, orders) should exhibit greater diversification, and this is in fact what we see. Taking into account the taxonomic uncertainties within these two groups we still find that the four large orders, Coleoptera et al., make up between 36–44% of all orders in the Holometabola, whereas the diverse Hemiptera comprise only 6–13% of the Hemimetabola.

More importantly, it should be recognized that the existence of other key innovations that may promote diversification within a given order is not mutually exclusive with the role of modularity. In fact, complete metamorphosis may it-

self have acted as a preadaptation or component subsequent key innovations. For example, the Coleoptera, Hymenoptera, Diptera, and Lepidoptera all happen to contain larvae that exhibit particularly early development and growth of wing imaginal discs compared to other holometabolous orders in which the growth of almost all imaginal primordia is suppressed until the very end of larval life (Nagy and Grbic 1999). Truman and Riddiford (1999) proposed that this additional degree of modularity between wing discs and other imaginal primordia could have been of adaptive significance in decreasing generation time in these four holometabolous orders, and therefore possibly contributing to their taxonomic success.

Another example of how variations in metamorphosis may contribute to adaptation and differential diversification in ways resembling “classic” key innovations may be found in the comparison of the Apocritan Hymenoptera and Cyclorhapan Diptera relative to their respective sister groups. The Apocrita and Cyclorhapa both exhibit an extreme form of metamorphosis in which all larval tissues are histolyzed and the whole adult body is formed from imaginal discs and histoblasts that proliferate during the pupal period (Gilliot 1995). Adoption of this radical developmental mode is correlated to massive radiations in relatively short periods of time in both these groups, producing over 80–90% of the species now present in their respective orders and a much broader diversity in larval and adult niches than present in their less metamorphic sister groups (Naumann 1991; Wiegmann et al. 1993b). The extreme metamorphosis in the Apocritan Hymenoptera, for example, facilitated the simplification of its larvae. This simplification may have been a key preadaptation for lifestyles, such as endoparasitism and sociality, that, in turn, likely enabled a remarkable radiation of the Apocritan Hymenoptera into novel ecological niches relative to their sister group.

While hemi- and holometabolous metamorphoses represent qualitatively different developmental processes, each developmental type itself encompasses a continuum of metamorphoses that vary in the degree of remodeling between the juvenile and adult stages (Svacha 1992; Sehnal et al. 1996; Nagy and Grbic 1999). From the above discussion, it is clear that these additional levels in metamorphic variation present at multiple taxonomic levels within the insects should provide a rich area in which to further explore the relationship between modularity and evolvability, and the influence they may have on long-term diversification in this extremely diverse group.

Although taxa that have evolved metamorphosis may be ideal systems for examining the role of temporal modularity in evolvability and diversification, the points outlined here should be equally applicable to the analysis of characters that exhibit spatial modularity within a given stage in ontogeny. The challenge will be to collect the data necessary to test

both predictions of the modular evolvability hypothesis—rates of diversification and phenotypic diversity—in taxa of interest. More generally, the outline presented here on modularity, evolvability, and diversification should contribute to the understanding of how the growing body of developmental data, and in particular the concept of developmental modules, can be put in a context relevant to phenotypic selection and phylogeny. Ultimately, such approaches will hopefully allow us to begin using developmental information to predict, rather than just to describe, patterns of evolution.

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