Introduction to Invertebrates

RECONSTRUCTION OF INVERTEBRATE PHYLOGENY
Cladistic Method

Downplaying the Linnean Categories
AN EXERCISE IN CLADISTICS
The study of invertebrates is a gateway to the vast diversity of animal life. The astronomical numbers and myriad forms of invertebrates delight the eye, challenge the mind, and provide limitless opportunities for scientific discovery. Invertebrates account for more than 99% of all species of animals and, although fewer than 1 million living species have been named so far, the total number of animal species on Earth may exceed 30 million. Clearly, most invertebrate species remain to be discovered and described, while among those already identified, few have been studied in depth. Thus, any curious individual equipped with the simplest observational or experimental tools can make original and enduring contributions to science.

At first glance, the diversity of invertebrates may seem incomprehensible, like contemplating infinity, but the countless individuals and species are variations on a relatively few readily identifiable themes. One of these themes is the ground plan (basic design, or Bauplan) of each taxonomic group. For example, although there are millions of species of arthropods, all have a segmented body, an exoskeleton that is molted with growth, and jointed appendages. Knowing these few traits enables anyone to identify an arthropod as such and to appreciate the insect, crustacean, centipede, and spider variations on the arthropod theme. The chapters in this book have been written to highlight the ground plan of each major group and thus to provide a foundation on which to understand the thematic variations.

Another way to simplify the diversity of invertebrates is to establish the evolutionary relationships between the groups of animals, to draw an evolutionary tree. This is accomplished by identifying similarities in the themes of two or more groups and uniting them on the basis of their unique similarities. So, for example, crabs, lobsters, and shrimps (and a few minor groups) are closely related to each other because only they, among all crustaceans, share a design with five pairs of locomotory appendages. The evolutionary history of a group is called its phylogeny and the actual depiction of evolutionary relationships is known as a phylogenetic tree (or cladogram). Although a phylogenetic tree, as a scientific hypothesis, is subject to testing and change, it nevertheless provides a framework on which to organize and compare ground plans and thus summarize much of the factual content of each chapter. For those unfamiliar with the method for constructing or interpreting phylogenetic trees, an exercise in phylogenetic reconstruction is provided later in this chapter.

Yet another approach to invertebrate diversity is to view animal design in a framework of functional principles. Here we seek to understand how the fundamental principles of physics and chemistry impose limits—indeed, control—design. For example, flight requires an airfoil (wing) to produce lift. Although the composition of wings can differ (exoskeleton, skin, feathers, aluminum) and the animals having them may be unrelated, all necessarily have the shape of a wing. Thus, we can predict that any animal that evolves flight will have something that looks like a wing. At a slightly more derived level are the principles of physiology, development, and ecology. These concepts together—physical, chemical, biological—allow one to view living invertebrates as complex and fascinating expressions of a few thematic variations. The subtlety and elegance of this approach breathes life into invertebrate zoology.

This book integrates invertebrate structure and function in an evolutionary context. The sequence of chapters, especially in the first part of the book, is progressive, and several chapters (those whose titles include “Introduction to”) describe major turning points in animal evolution, such as the origin and significance of the multicellular body and, later, bilateral symmetry. At each of these “steps,” the animal body evolved a radically new design, which created novel ecological opportunities and was inherited by all descendants. How those new designs might have evolved, how they work in the context of general functional principles, and how they enabled their possessors to exploit new adaptive zones are the subjects of the “Introduction to” chapters. This book, then, is a blend of factual descriptions and provisional syntheses that are subject to scientific testing and revision. Throughout the book, we emphasize that opportunities abound for discovery in this dynamic field.

To provide comprehensive coverage of invertebrates is a goal of this book, but a few taxa are described in less detail than others. Because most schools have specialized courses in protozoology, parasitology, and entomology, we provide only abbreviated coverage of unicellular organisms (protozoa), parasitic invertebrates, and insects (Hexapoda).

**RECONSTRUCTION OF INVERTEBRATE PHYLOGENY**

**CLADISTIC METHOD**

One of the noteworthy achievements of biological research has been the establishment of a natural system, the recognition of species and the arrangement of those species in a hierarchical pattern of relationships. This pattern of evolutionary or kinship relationships is called a phylum or order, or a “tree of life.”

The science that concerns itself with the discovery and depiction of phylogeny is known as phylogenetic systematics or cladistics. The goal of cladistics is to discover and portray the kinship relationships among species, ultimately in a phylogenetic tree, or cladogram.

In practice, one establishes a kinship relationship between two named groups, or taxa (the singular is taxon), by detecting a trait, or character, that is expressed in these taxa alone. Such a uniquely shared character is called a synapomorphy (= shared derived character), and taxa united by one or more synapomorphies are called sister taxa. Because a synapomorphy is shared by the sister taxa and no other taxon, it must have evolved in the immediate ancestor of the sister taxa. Thus the synapomorphy observed in the descendants actually originated in the ancestor as an evolutionary novelty, now called an autapomorphy (= self-derived character). As the sole descendants of that one immediate ancestor, the sister taxa constitute a monophyletic (= one origin) taxon. The ultimate goal of cladistics is to reconstruct a comprehensive tree of life based solely on monophyletic taxa.

An example of these concepts can be drawn from the arthropods (Fig. 1-1). For taxa, consider the crustaceans (such as shrimps, crabs, and lobsters) and tracheates (insects, milli-
FIGURE 1-1 Cladistics. Example of the use of cladistics in phylogenetic reconstruction (see text). The observation of a uniquely shared character (synapomorphy), “mandibles,” in Crustacea and Tracheata unites them as sister taxa in a monophyletic taxon, Mandibulata. Thus the stem species, or ancestor, of Mandibulata must have first expressed “mandibles” as an evolutionary novelty (autapomorphy). Similarly, the observation that “jointed appendages” occur in only chelicerates and mandibulates and nowhere else indicates that the character “jointed appendages” is a synapomorphy of a synapomorphy of the sister taxa, which form the monophyletic taxon Arthropoda. The ancestral arthropod, therefore, first acquired “jointed appendages” as an evolutionary innovation, or autapomorphy. If an observer, for lack of complete knowledge, unites chelicerates and crustaceans into what he believes is a monophyletic taxon because both share “jointed appendages,” the union is false because “jointed appendages” are not unique to chelicerates and crustaceans alone, but to all arthropods. Thus the character “jointed appendages” did not evolve in the immediate ancestor to chelicerates and crustaceans alone, but in a deeper ancestry that also gave rise to the tracheates. The chelicerates and crustaceans express this deeply ancestral trait as a shared primitive character, or symplesiomorphy. The false union based on a symplesiomorphy is called a paraphyletic taxon. The autapomorphy “chelicerae” is a pair of pincerlike appendages on the second segment of the head.

A properly constructed phylogenetic tree is a deeply informative representation. The kinship relationships of species and higher taxa are shown graphically and the synapomorphies are indicated for each pair of sister taxa. The autapomorphies associated with stem species, moreover, offer insight into the form of the ancestors, which then may be compared with fossil evidence, if such exists.

Although we try to choose simple, factually sound examples to explain the method of phylogenetic reconstruction, in practice most reconstructions are more complex. It often happens, for example, that apparent synapomorphies are contradictory: Synapomorphy 1 unites taxa A and B and synapomorphy 2 unites taxa B and C. This results in two different and competing trees. In this situation, systematists choose the tree

- Arthropoda
  - Chelicerata
  - Mandibulata
  - Crustacea
  - Tracheata

Thus the character “jointed appendages” did not evolve in the immediate ancestor to chelicerates and crustaceans alone, but also by the tracheates. This means that the “jointed appendages” of chelicerates and crustaceans is not a shared derived character but rather a shared ancestral trait, or symplesiomorphy, that evolved in the stem species (ancestor) of all arthropods. The erroneous union of crustaceans and chelicerates based on a symplesiomorphy is called a paraphyletic taxon (Fig. 1-1). A paraphyletic taxon contains some, but not all, of the descendants of the stem species. A major challenge of modern phylogenetic research is to identify and weed out paraphyletic taxa. In this example, “jointed appendages” is actually an autapomorphy of the monophyletic taxon Arthropoda, which includes the sister taxa Chelicerata and Mandibulata (Crustacea + Tracheata; Fig. 1-1).

A paraphyletic taxon fails to include all descendants of one ancestor, but a polyphyletic taxon includes the descendants of more than one ancestor. This mistake occurs when a shared similarity results from evolutionary convergence rather than common ancestry. Similarity attributable to common genetic inheritance is called homology, whereas the superficial similarity that arises from convergence is known as homoplasy (or analogy). Only homologous structures are useful in phylogenetic reconstruction based on monophyletic groups. An example of a polyphyletic taxon would be one that united birds, bats, and insects together because all share “wings.” Bird wings, bat wings, and insect wings, however, are unrelated homoplous structures, and the members of this polyphyletic taxon descended from three separate ancestors, each of which independently evolved its own unique wing.

The application of the cladistic method to species, groups of species, and groups of groups of species leads to the dichotomously branching hierarchic structure that typifies a phylogenetic tree. Hierarchic structure means that species are nested in larger, more inclusive taxa, which are contained in still more inclusive groups. So a species of shrimp is a kind of crustacean, which is a kind of mandibulate, which is a kind of arthropod, which is a kind of animal. The hierarchy shown in Figure 1-1 can also be summarized in tabular form in a phylogenetic hierarchy:

- Arthropoda
  - Chelicerata
  - Mandibulata
  - Crustacea
  - Tracheata

pedes, and centipedes, for example). Representatives of these two taxa show that all share the character “mandibles” (jaws derived from appendages on the third head segment), which occurs nowhere else and thus is a synapomorphy of crustaceans and tracheates. The synapomorphy indicates that the sister taxa (Crustacea, Tracheata) constitute a monophyletic taxon, the ancestor of which first evolved mandibles as an evolutionary novelty, or autapomorphy. Once the monophyletic taxon has been identified, it is given a formal name—in this case, Mandibulata.

Now suppose that, instead of crustaceans and tracheates, the study began with crustaceans and chelicerates (including horseshoe crabs, scorpions, and spiders) and found that they shared the character “jointed appendages,” which was then hypothesized to be a synapomorphy of the two taxa (Fig. 1-1). The character “jointed appendages,” however, is not shared by crustaceans and chelicerates alone, but also by the tracheates. This means that the “jointed appendages” of chelicerates and crustaceans is not a shared derived character but rather a shared ancestral trait, or symplesiomorphy, that evolved in the stem species (ancestor) of all arthropods. The erroneous union of crustaceans and chelicerates based on a symplesiomorphy is called a paraphyletic taxon (Fig. 1-1). A paraphyletic taxon contains some, but not all, of the descendants of the stem species. A major challenge of modern phylogenetic research is to identify and weed out paraphyletic taxa. In this example, “jointed appendages” is actually an autapomorphy of the monophyletic taxon Arthropoda, which includes the sister taxa Chelicerata and Mandibulata (Crustacea + Tracheata; Fig. 1-1).

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with the fewest branches, the tree that assumes the fewest number of character changes—that is, the most parsimonious tree. This principle of **parsimony** is one of the important underlying assumptions of phylogenetic systematics (and of science in general). It is an especially important tool in computer-aided cladistics. In such analyses, the software sifts through large amounts of data in the form of numerically coded morphological and molecular characters and, using different routines for joining or weighting them, generates more than one tree. From among these alternatives, a most parsimonious tree is typically calculated and drawn.

In this book, all trees of phylogenetic relationship are based on synapomorphies and, unless otherwise noted, are plotted by hand, as in Figure 1-1. This explicit and direct approach was adopted to allow you, the student, to evaluate the choice and validity of characters used in the reconstructions. Trees are sensitive to new facts and to reevaluation of assumptions about the nature of the characters themselves. As you acquire new knowledge applicable to phylogenetics, create your own trees and test them against those presented in the text.

### DOWNPLAYING THE LINNÉAN CATEGORIES

Modern cladistics is the method of choice for establishing kinship relationships among taxa. Once monophyletic taxa are identified and named on a phylogenetic tree or in a phylogenetic hierarchy, the hierarchic relationships among the taxa are obvious and clear (see Fig. 1-1 and the phylogenetic hierarchy set out in the last section). The question then is: “What is gained by assigning a Linnaean category—phylum, class, order, and so on—to the taxon names already present?” Many systematists today have abandoned the Linnaean categories because they are unnecessary, because they were established by Linnaeus for what he considered to be the immutable levels of Creation, and because new cladistic ranks of many taxa do not coincide well with the old Linnaean categories. For some, liberation from the Linnaean categories will continue to provide a familiar and constant frame of reference.

This book embraces the new cladistic approach to systematics and largely dispenses with Linnaean categories. The relative ranks of taxa can be obtained from the phylogenetic taxa, the text sections that include “Phylogenetic Hierarchy of” in their title, and the chapter headings. To soften the transition from the classical to modern approach, however, Linnaean categories are assigned to taxa as superscript abbreviations when a taxon name is used as a text heading. The standard abbreviations are: \( ^{\underline{2}} \) for phylum, \( ^{\underline{3}} \) for Class, \( ^{\underline{4}} \) for Order, and \( ^{\underline{5}} \) for Family. An uppercase \( ^{\underline{5}} \) prefixed to a category abbreviation identifies a supertaxon, a lowercase \( ^{\underline{1}} \) identifies a subtaxon, and a lowercase \( ^{\underline{2}} \) indicates an infrataxon. Supert-, sub-, and infrataxa are ranked as follows:

- **Supertaxon**
  - Taxon (for example, phylum, class, order)
- **Subtaxon**
  - Infrataxon

In the phylogenetic hierarchy given earlier, the superscripts would be: Arthropoda\(^{\underline{2}}\), Chelicerata\(^{\underline{3}}\), Mandibulata\(^{\underline{4}}\), Crustacea\(^{\underline{5}}\), and Tracheata\(^{\underline{2}}\).

### AN EXERCISE IN CLADISTICS

Figures 1-2, 1-3, and 1-4 as well as the following text provide an exercise in cladistics for those who wish to practice building a phylogenetic tree. The exercise is divided into three steps, each of which is highlighted and explained here and in the figure legends.

- **Step 1: Study characters of a group of taxa in question and search for apomorphies, first within species (Fig. 1-2)**

  Figure 1-2 shows one individual from each of six fictitious species. The first task is to establish (or not) the uniqueness (validity) of each species. To accomplish this, search for a character that is expressed uniquely in each species alone. Once identified, that character is assumed to have evolved as an evolutionary novelty in the ancestor of that species and is thus a species-level autapomorphy. An autapomorphy for each of the six species is shown in Figure 1-2. In this example, these species are then named appropriately according to their autapomorphies. So, the species with the autapomorphy “fan tail” is named *Fan tail*, the species with “long antennae” is named *Long antennae*, and so on as shown in Figure 1-2. The italicized species binomial always consists of a capitalized genus name (for example, *Fan*) and a lowercase species name (*tail*). In actual practice, both names would be latinized.

- **Step 2: Find synapomorphies that link species and groups of species pairwise into a most parsimonious tree (Fig. 1-3)**

  Figure 1-3 shows the most parsimonious phylogenetic tree for the six species. The tree results from the recognition of a character or characters (synapomorphies) that are shared uniquely by two species or two groups of species. Notice that at least one synapomorphy supports the pairwise union of species (and higher groups) into sister taxa. For example, species *Shoulder leg* and *Fan tail* are united in a monophyletic taxon by the uniquely shared character (synapomorphy) “stalked eyes.” This new monophyletic taxon has yet to be named and thus is temporarily designated *Nomen nominandum* (= new name), abbreviated N. N.

  Proceeding deeper into the tree, notice that the monophyletic taxon that includes *Shoulder leg* and *Fan tail* is united with the species *Scissors tail* in another monophyletic taxon by the synapomorphies “three segments” and “pliers claw.” This new, higher-level taxon is also temporarily designated N. N.

  Figure 1-3 shows the progressive pairing of taxa into monophyletic groups based on shared derived characters. But a dilemma is encountered with *Paddle foot* at the base of the
tree. The dilemma is whether the characters associated with *Paddle foot* are plesiomorphies or apomorphies. Is the character “paddle foot” an autapomorphy of *Paddle foot* that is found in that species and nowhere else, or is it a symplesiomorphy occurring in *Paddle foot* and in other, as yet unstudied species? Similarly, is the character “eight segments” an autapomorphy of the original six species or is it a symplesiomorphy occurring in those six plus additional species? The questions boil down to this: How do we establish the apomorphy vs. plesiomorphy polarity of the characters? The monophyly or paraphyly of the group of six species hinges on the determination of character polarity. The practical solution to this dilemma is to discover whether or not “eight segments” and “paddle foot” occur outside the group of six species, and this requires the examination of additional species. The extension of the cladistic analysis beyond the taxa of immediate interest is called an outgroup comparison. The goal is to determine character polarity to resolve the plesiomorphy vs. apomorphy dilemma.

- **Step 3: Perform an outgroup analysis and name the monophyletic taxa (Fig. 1-4)**

Figure 1-4 resolves the uncertain polarity of characters “paddle foot” and “eight segments” by performing an outgroup analysis. The outgroup in this example is represented by a single unnamed species and it is compared with the ingroup consisting of the six original species. The outgroup species lacks the characters “paddle foot” (it has “normal” feet) and “eight segments” (it has nine segments). Thus, the outgroup comparison enables us to conclude that “paddle foot” is an autapomorphy of the species *Paddle foot* and “eight segments” is a synapomorphy of *Paddle foot* and the taxon (*Cultrichela*) that includes the remaining five ingroup species. Not all species of *Cultrichela*, however, have eight segments. Some have evolved a body with fewer segments, in this example, five and three segments. Or, alternatively, “eight segments” is an autapomorphy of a monophyletic taxon that includes the original six species. The character “eight segments,” as both synapomorphy and autapomorphy, is shown in Figure 1-4.

In reference to the original analysis, the ingroup of six species, apomorphies now support the monophyly of all sister taxa. At this point, it is appropriate to replace the provisional N. N. designation with a formal Latin name. These formal names, which are derived from taxon autapomorphies, are shown on Figure 1-4. For example, the monophyletic taxon supported by the apomorphy “stalked eyes” is named Exophthalmia (= prominent eyes), the taxon supported by “three segments” is named Triannelida (= three rings), and the monophyletic taxon that includes all six species, based on the apomorphy “eight segments,” is designated Octoannelida (= eight rings). The phylogenetic hierarchy of Octoannelida is:

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Octoannelida
Paddle foot
Cultrichela
Long antenna
Urocopa
Five segments
Triannelida
Scissors tail
Exophthalmia
Shoulder leg
Fan tail
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FIGURE 1-3 Exercise in cladistics, step 2 (see also text). The six fictitious species are united pairwise into monophyletic taxa on the basis of uniquely shared characters (synapomorphies). The observed synapomorphy of each pair of sister taxa (together a monophyletic taxon) evolved as an evolutionary novelty in the ancestor of the monophyletic taxon and is indicated on the tree as an autapomorphy. Each of the monophyletic taxa is given a general temporary designation, abbreviated N. N. Notice the uncertainty associated with the characters "eight segments" and "paddle foot." Both characters could be either apomorphies or plesiomorphies. If they are apomorphies, then the N. N. taxon that includes all six species is monophyletic; if they are plesiomorphies, then the taxon is paraphyletic. The plesiomorphic vs. apomorphic interpretation of these characters can be resolved only by comparison with a taxon or taxa outside this group of six species. Such an outgroup comparison is shown in Figure 1-4 and is described in the text.
FIGURE 1-4  Exercise in cladistics, step 3 (see also text). An outgroup analysis shows that the character “paddle foot” is an autapomorphy of the species Paddle foot. It also indicates that the character “eight segments” is a synapomorphy of the taxon (species) Paddle foot and its sister taxon, Cultrichela, which includes all other species. Thus the synapomorphy “eight segments” establishes the monophyletic taxon Octoannelida for the six species in this study. The autapomorphies of the monophyletic taxa are:

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Lab Manuals


Morphology


Functional Morphology and Physiology


Ecology

References


Reproduction, Development, Larvae, and Metamorphosis


Cladistics and Evolution


Paleontology

Moore, R. C. (Ed.): 1953–1966. Treatise on Invertebrate Paleontology. Geological Society of America, University of Kansas Press, Lawrence, KS. (Eighteen volumes.)

Field Guides


INTERNET SITES

General

http://life.bio.sunysb.edu/marinebio/mnbweb.html (State University of New York. Invertebrate images, references, career opportunities, and news regarding marine biology.)

http://animaldiversity.ummz.umich.edu/index.html (University of Michigan Museum of Zoology Animal Diversity Web.)

http://www.ucmp.berkeley.edu/dr_web/newsite/phylogeny.html (Take the Web Lift to Taxa to discover the relationships that connect all organisms.)

http://www.usnh.si.edu/departments/invert.html (Smithsonian National Museum of Natural History. Good coverage of certain groups of invertebrates, such as squids and their relatives.)

http://www.george-tnnese.edu/Museum/zoology/Prado.html (Explore the relationships that connect all organisms.)


http://www.marine.stanford.edu/HMSweb/careers.html (Marine biology links, careers, and more.)

http://www.ucmp.berkeley.edu (University of California at Berkeley Museum of Paleontology. Explore their invertebrate collections and follow links to impressive images of living invertebrates.)

http://www.mnh.si.edu/departments/invert.html (Smithsonian National Museum of Natural History. Good coverage of certain groups of invertebrates, such as squids and their relatives.)

http://mbayaq.org (Monterey Bay Aquarium. The next best thing to being there. Explore their beach, rocky intertidal pool, open water, and kelp forest exhibits, several of which are three-dimensional and several that are interactive.)


Lab Manual

http://www.lander.edu/rsfox/310labindex.html (Lander University Online Invertebrate Lab. Illustrated anatomical descriptions of approximately 100 species in support of invertebrate teaching and research.)

Professional Societies

http://www.invertebrates.org (American Microscopical Society. Publishes the international journal Invertebrate Biology. The journal’s Web site links to other sites on invertebrates and opportunities in the field for research, jobs, and education.)

http://www.museum.unl.edu/asp (American Society of Parasitologists. Much useful information and many images at their Web site.)

Cladistics

http://www.treeoflife.org/tree/phylogeny.html (Tree of Life. Provides a phylogenetic classification of all taxa of living organisms based on molecular and morphological traits. Coverage is uneven and often outdated, but new information is being added constantly. Good source of contemporary references to invertebrate systematics.)


http://www prevailed/evolution/Cladistics.html (Tree of Life. Provides a phylogenetic classification of all taxa of living organisms based on molecular and morphological traits. Coverage is uneven and often outdated, but new information is being added constantly. Good source of contemporary references to invertebrate systematics.)


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