SYSTEMATIC ZOOLOGY: INVERTEBRATES

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Summary

The exuberant diversity of the animal kingdom (Metazoa) is primarily manifested in the realm of invertebrates. This contribution introduces invertebrate diversity by briefly surveying the thirty-odd groups known as animal phyla. The emphasis is on our current understanding of the evolutionary relationships of the animal phyla on the basis of both morphological and molecular data. The emphasis will be on extant rather than extinct organisms.

1. Introduction to the systematic zoology of the Metazoa (Animalia)

Although no one will dispute the manifest importance of the vertebrates in the scheme of nature, vertebrates are easily eclipsed in sheer variety by the invertebrates that make up the vast majority of animal or metazoan biodiversity. Of a total of one to two million described animal species, a mere 45.000 are represented by vertebrates. This stupendous diversity of invertebrates furnishes a rich playing ground for all manner of biological research. From this diversity of forms, biologists have selected so-called model system species according to their special suitability for studying particular biological problems. Familiar examples include the fruit-fly *Drosophila melanogaster* that is used in wide ranging experiments from population biology to developmental genetics, and the nematode *Caenorhabditis elegans* that is the subject of intense efforts to characterize its entire genome. However, model systems represent only a small fraction of the available diversity of animals. This paper will put the model systems into perspective by presenting an introductory survey of all animal phyla, emphasizing their evolutionary relationships.

One of the prime objectives of the science of systematic zoology is the reconstruction of the hidden evolutionary history of the animal kingdom. The emphasis is on recovering the pattern of evolutionary branchings that defines the structure of the tree of relationships within the animal kingdom. The task is daunting. Currently more than a million species of living animals have been described, although the exact number remains unknown, and estimates for the real biodiversity of animals invariably yield even higher figures. Fortunately, this exuberant diversity is not completely chaotic. Animals can be grouped into taxa of increasing inclusiveness on the basis of possessing specific sets of shared derived characters. The animal phyla traditionally represent the most inclusive or highest level animal taxa in the traditional Linnaean classificatory system, and these are clearly demarcated from each other by the possession of unique body plans or ground patterns. The distinctiveness of the animal phyla stands in sharp contrast to our ability to accurately reconstruct their evolutionary relationships, which have roots more than 500 million years old when the major groups of animals diverged. A long history extending back at least to the period immediately following the publication of Charles Darwin's *On the origin of species* in 1859 richly illustrates our extensive struggles to trace life's ancestry. Although the core practice and concerns of systematic zoology have remained relatively unchanged for almost one and a half centuries, the continual gathering of more data, and the development of new techniques and methods of analysis have allowed the tapping of virgin data sources. These in turn have stimulated the study of old problems from new perspectives. Technological advances, such as the development of electron microscopy and molecular biology, have opened up a wealth of unexplored data. In addition, the widespread adoption of cladistics as a uniform method of phylogenetic inference has greatly benefited the comparability and testability of proposed phylogenetic hypotheses. Because phylogenetic hypotheses place inescapable constraints upon scenarios of animal body plan evolution by specifying a mandatory sequence of origins and divergences of animal body plans, an understanding of the pattern of animal relationships is therefore essential for any study that addresses questions of evolutionary process.

We present here a concise overview of the current understanding of invertebrate systematics on the basis of both molecular and morphological data. The following section on Animal phylogeny: data sources and interpretation summarizes what information is used to reconstruct higher level animal relationships. The section on

Systematic zoology of the Metazoa summarizes our current understanding of the systematics of all recognized animal phyla. The section on Alternative hypotheses of metazoan relationships summarizes and complements the discussions of the preceding sections, with an emphasis on the difficulties that are encountered by using different data sources. Technical terms (including names of supraphyletic taxa) are explained either in the text or the glossary. The following discussions deal almost exclusively with extant taxa. Fossils are only considered when they have offered unique insights into the origin of a phylum or supraphyletic taxon (e.g., Arthropoda, Brachiopoda).

2. Animal phylogeny: data sources and interpretation

For a general exposition of the fundamentals of systematic research, we refer the reader to the various relevant subsections under Classification and diversity of life forms. In principle, any observable attribute of animals that exhibits an appropriate level of variation could be used for reconstructing phylogenetic relationships. Traditionally, a qualitative distinction is made between morphological and molecular data. This distinction should not be regarded as absolute, since many of the same problems of analysis and issues of interpretation are common to both types of data.

2.1 Morphology

The field of invertebrate systematics may seem forbidding to the uninitiated reader as a result of the jargon riddled literature. An imposing quantity of terms is used both to describe the detailed morphology of organisms, as well as to designate taxa or clades of strictly defined membership. Luckily, there exists at least some logical connection between these realms of nomenclature. Many of the names attached to certain clades of invertebrates reflect the nature of the underlying characters used to define these taxa. Therefore we will provide a succinct overview of some of the most important metazoan clades, and the key features that have been marshalled in their support. This will at the same time introduce the reader to some household names of animal clades, and some very basic knowledge of animal organization.

One of the deepest splits within the animal kingdom separates the Bilateria (Figure 6, 10) or bilaterally symmetrical animals from those that lack this body symmetry. The same division can be made when we consider the presence of embryonic germ layers. A synonym of Bilateria is Triploblastica, which refers to the presence of three germ layers: ectoderm (outer layer forming skin and nervous system), endoderm (inner layer forming the digestive system), and mesoderm (middle layer forming most other tissues and organs). Consequently, animals lacking mesoderm but possessing ecto- and endoderm can be referred to as Diploblastica.

One of the fundamental splits within Bilateria is traditionally based upon embryological data: Protostomia and Deuterostomia (Figure 6, 7, 8). Most animals develop from a more or less hollow sphere of cells, called a blastula, into a layered structure called a gastrula by invaginating the embryonic gut or archenteron. This process can be understood in analogy to pushing a finger into a blown-up balloon to produce an invagination. The opening of the archenteron to the outside is called blastopore, which will develop into the mouth in Protostomia (meaning mouth first) and the anus in

Deuterostomia (meaning mouth second).

A different but very important distinction between bilateral animals has been made upon the basis of the nature of their main body cavities. In Coelomata, the middle germ layer or mesoderm forms a cavity which becomes lined with an epithelium. The body cavities that house our own internal organs are examples of coeloms. This organization is very different from animals that lack a coelom, the non-coelomates. These have traditionally been separated into Pseudocoelomata (possessing a body cavity not lined with mesodermal epithelium), and Acoelomata (having a compact organization without a body cavity).

Many bilaterians possess ventrally (belly side) located main nerve cords. These taxa have been called Gastroneuralia. This contrasts with the dorsal (back side) position of the main nerve cord in for example our own phylum, Chordata.

Much phylogenetic significance has been attached to the mode of embryonic cleavage, the process during which the fertilized egg divides to become multicellular. Based upon the geometry of cleavage cells (called blastomeres), one can at least distinguish spiral cleavage, and radial cleavage. A taxon Spiralia (a major group of protostomes) (Figure 8) is based upon the former, a taxon Radialia (almost identical to Deuterostomia) is based upon the latter cleavage type.

2.2 Molecules

Molecular studies of invertebrate systematics are currently dominated by the use of 18S rRNA/DNA nucleotide sequences. The 18S rRNA molecules are structural components of ribosomes, which are the protein synthesis factories of living cells. For most phyla at least one species has been sequenced, and for several phyla multiple species have been sequenced for analyses of intra-phylum relationships (e.g., arthropods, chordates). Nevertheless, a host of new molecular data sources are increasingly being used.

Recently, comparative studies of both temporal and spatial aspects of gene expression patterns of a plethora of identified developmental genes have added an extra dimension to higher level animal phylogenetics. Comparative developmental gene expression studies currently form the core of the blossoming discipline of evolutionary developmental biology, and have already generated fundamental evolutionary insights. One of the most tantalizing findings of these new studies is evidence for a complete inversion of the dorsoventral (back to belly) axis in invertebrates. This means that the ventral side of a fly is directly comparable and homologous to the dorsal side of a vertebrate! Zoologists are now busy searching for corroborative evidence from morphology, and try to pinpoint exactly when and where in the metazoan tree such a dramatic event could have taken place.

2.3 Fossils

Although the fossil record provides the only direct source of information for testing different hypotheses about the course of evolution, fossils have nevertheless not played a leading role in current attempts to reconstruct higher level metazoan phylogeny.

Generally, invertebrate zoology textbooks provide a rather pessimistic assessment of the role of the fossil record in understanding the origin and nature of animal diversity. This perspective is not entirely justifiable. Despite the fact that the fossil record largely remains silent about the evolution of most animal phyla, fossils have nevertheless provided fascinating insights into the diversity and/or evolutionary origin of various extant phyla, including poriferans, ctenophores, arthropods, molluscs, priapulids, echinoderms, chordates, and brachiopods. Especially relevant are Cambrian fossils of exceptional preservational quality found in diverse assemblages all over the world, such as the Burgess Shale fauna of British Columbia, the Sirius Passet fauna of northern Greenland, and the Chengjiang fauna of southwest China. As will be illustrated in relevant places below, the rigorous application of stem and crown group concepts (see Glossary) is an important handle for helping to systematize these findings. But admittedly, the phylogenetic significance of many fossils remains elusive, in particular the highly problematic Ediacaran (Precambrian) fossils, which may be a diverse assemblage that contains genuine members of extant phyla, and real oddballs that cannot be placed inside the Metazoa.

3. Systematic zoology of the Metazoa

We will provide an overview of the current knowledge of the systematics of all recognized animal phyla. The emphasis will be on the results from recent cladistic studies of both morphological and molecular data, without detailing the relative merit of all published alternative hypotheses. We have attempted to make this survey readable for non-specialists by keeping technical discussions of morphology and molecules to a bare minimum. The subsections treat several more or less closely related phyla simultaneously, discussing their monophyly and probable sister group relationships, and where relevant, the internal phylogenetic relationships of individual phyla. Broader scale phylogenetic patterns are discussed under Alternative hypotheses of metazoan relationships. For taxon-specific details of morphology, behavior, ecology, evolution, and biogeography, the reader is referred to the specialist chapters on the respective phyla elsewhere in the encyclopedia.

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Biographical Sketches

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