Systematics

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Systematics is the study of biological diversity that has as its primary goal the reconstruction of phylogeny, the evolutionary or genealogical history of particular group of organisms (e.g., species). Because of its emphasis on phylogeny, this discipline is often referred to as phylogenetic systematics or cladistics. Other related goals of systematics include determination of the times at which species originated and became extinct and the origin and rate of change in their characters. An important component of systematics is taxonomy that involves the identification, description, nomenclature, and classification of organisms. Systematics provides a framework for interpreting patterns and processes in evolution using explicit, testable hypotheses.

The rapid pace of research on marine mammals has resulted in renewed interest in their systematics. Phylogenetic systematic methodology as introduced here has gained near universal acceptance. [For a general introduction see Maddison and Maddison (2000) and for more detailed discussion of methods see Felsenstein (2004).] In addition to their use in elucidating evolutionary relationships, phylogenies are now recognized as powerful tools for unveiling evolutionary patterns of biodiversity in ecological and behavioral settings (Brooks and McLennan, 2002).

I. Basic Tenets of Phylogenetic Systematics

The recognition of patterns of relationship among species is founded on the concept of evolution. Patterns of relationship among species are based on changes in the characters of an organism. Characters are diverse, heritable attributes of organisms that include DNA base pairs, anatomical and physiological features, and behavioral traits. Two or more forms of a given character are termed the character states. For example, among pinnipeds the character, contact between the maxillary and frontal bones consists of three character states: (1) V-shaped (in bears, extinct desmatophocids, *Enaliarctos*, and phocids), (2) W-shaped (in otariids), and (3) transverse (walruses). In the determination of relationships among groups of organisms phylogenetic systematics emphasizes evolutionary novelties (derived characters) in contrast to ancestral similarities (primitive characters). If derived characters are unique to a particular taxon rather than showing relationships among taxa they are termed autapomorphies. An example of an autapomorphy is the straight contact between the maxillary and frontal bones seen only in walruses among pinnipedimorphs (living pinnipeds and their fossil relatives).

The evolutionary history of a group of organisms can be inferred by sequentially linking species together based on their common possession of derived characters, also known as synapomorphies. These derived characters are considered to be homologous, a similarity that results from common ancestry. For example, the flipper of a seal and that of a walrus are homologous because their common ancestor had flippers. In contrast to homology, a similarity not due to homology is homoplasy. For example the flipper of a pinniped and that of a whale are homoplasious as flippers because their common ancestor lacked flippers. Homoplasy may arise in one of two ways convergence (parallelism) or reversal. Convergence is the independent evolution of a similar feature in two or more lineages. Thus seal flippers and whale flippers evolved independently as swimming appendages, their similarity is homoplasious by convergent evolution. Reversal is the loss of a derived feature coupled with the reestablishment of an ancestral feature. For example, in phocine seals (e.g., bearded seal, hooded seal, and the Phocini) the development of strong claws, lengthening of the third digit of the foot, and de-emphasis of the first digit of the hand are character reversals because none of them characterize phocids ancestrally but are present in terrestrial arctoid carnivores, common ancestors of pinnipeds.

Relationships among organismal groups are commonly represented in the form of a cladogram, a branching diagram that conceptually represents the best estimate of phylogeny (Fig. 1). Derived characters are used to link monophyletic groups, groups of taxa that consist of a common ancestor plus all descendants of that ancestor (referred to as a clade). For example, currently the best supported hypothesis of relationships among pinnipedimorphs based on both morphologic and molecular characters proposes that phocid seals (Phocidae) and an extinct lineage (Desmatophocidae) are more closely related to each other than either is to other pinnipeds. Fur seals and sea lions (Otariidae) together with their sister taxon walruses (Odobenidae) are positioned as the next closest relatives to this clade with the fossil taxon *Enaliarctos* recognized as the most basal lineage (Fig. 1). According to this hypothesis, relationships among pinnipedimorphs are depicted as sets of nested hierarchies. In this case, four monophyletic groups can be recognized. The most exclusive monophyletic group is that formed by phocid seals and desmatophocids since this clade shares derived synapomorphies not also exhibited by walruses, otariids or *Enaliarctos*. At the other extreme, the most inclusive monophyletic group is that formed by *Enaliarctos* (Otariidae + Odobenidae) (Desmatophocidae + Phocidae).

The task in inferring a phylogeny for a group of organisms is to determine which characters are derived and which are ancestral. If the ancestral condition of a character or character state is established, then the direction of evolution from ancestral to derived, can be inferred, and synapomorphies can be recognized. The methodology for inferring direction of character evolution is critical to cladistic analysis. Outgroup comparison is the most widely used procedure. It relies on the argument that a character state found in close relatives of a group (the outgroup) is likely to be the ancestral or primitive state for the group of organisms in question (the ingroup). Usually more than one outgroup is used in an analysis, the most important being the first or genealogically closest outgroup to the ingroup called the sister group. For example, among pinnipedimorphs the ingroup includes Phocidae (seals), Desmatophocidae (extinct seal relatives), Otariidae (fur seals and sea lions), Odobenidae (walruses), and the fossil taxon *Enaliarctos*. Phocidae is hypothesized as the sister group of Desmatophocidae and these taxa together form the sister taxon to Odobenidae + Otariidae. *Enaliarctos* is positioned as the earliest diverging lineage. Ursids (bears) are hypothesized as the closest pinniped outgroup (Fig. 2) although there is evidence to support an alternative arrangement, an ursid-mustelid ancestry.

II. Phylogeny Reconstruction

The first step in the reconstruction of phylogeny of a group of organisms is selection and definition of characters and character states for each taxon (e.g., species). Next, the characters and their states are arranged in a data matrix (Table I). Characters can be further distinguished; those with two states are binary, whereas characters with three or more states are multistate. For each character, ancestral and derived states are determined. The determination of character state, whether ancestral or derived (also called polarity assessment) is done using outgroup comparison. For example, if the distribution of character 1, condition of the lacrimal bone, is considered, two character states are recognized, the presence versus the absence (or fusion of the lacrimal such that it does not contact the jugal). The outgroup bears possess a lacrimal bone condition which is the ancestral state (Table I). The ingroup taxa lack the lacrimal bone which is the derived condition. Since this derived state unites pinnipedimorphs to the exclusion of bears it is considered a synapomorphy.

A final step in phylogeny reconstruction is the construction of a cladogram or phylogenetic tree by sequentially grouping taxa based on the common possession of one or more shared derived character states (Fig. 3 A-C) (three possible pinnipedimorph cladograms). An important aspect of phylogeny reconstruction is the principle of parsimony. The basic tenet of parsimony is that the cladogram that contains the fewest number of evolutionary steps, or changes between character states of a given character summed for all characters, is accepted as being the best estimate of phylogeny. However, multiple equally parsimonious solutions are possible and should be examined as well as suboptimal topologies (i.e., less parsimonious trees). In this example, Fig. 3B is the most parsimonious cladogram. Note that an alternative cladogram for the data set (Fig. 3C) showing a different relationship among the five taxa, requires eight characters state changes, two more than the most parsimonious cladogram (Fig. 3B). It should be noted that this alternative view, an alliance between the walrus and otariids, although less parsimonious on the basis of morphologic characters in the data set employed herein, is consistently and robustly supported by molecular data and total evidence analysis. It also should be pointed out

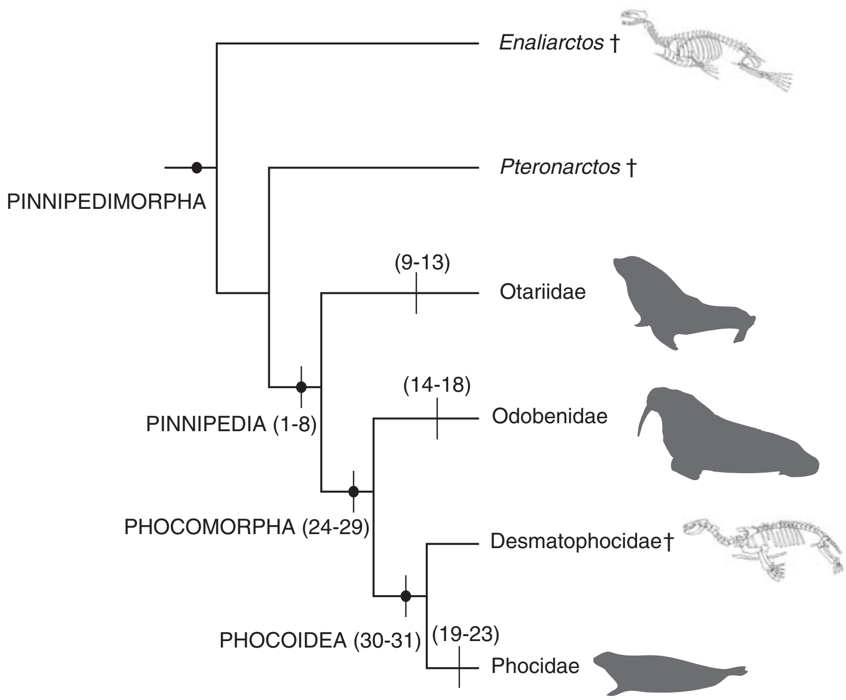

Figure 1 *Hypothesis of pinnipedimorph relationships modified from Berta* et al., *2006. † = extinct taxa.*

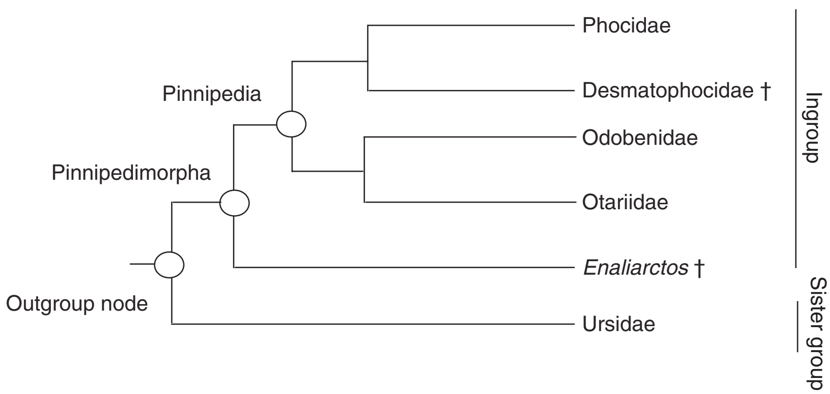

Figure 2 *Pinniped relationships with ingroup and outgroups identified. † = extinct taxa. Although ursids are hypothesized as the closest outgroup there is evidence to support an ursid-mustelid ancestry for pinnipeds.*

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TABLE I
Data Set for Analysis of Pinnipedimorphs Plus an Outgroup Showing Five Characters and Their Character States

	Character/character states				
Taxon	*Lacrimal bone*	*Middle ear bones*	*Orbital/maxilla*	*Maxilla/frontal*	*Squamosal/jugal*
Outgroup					
Ursids	Present	Small	No	V shape	Overlapping
Ingroup					
Enaliarctos	Absent	Small	No	V shape	Overlapping
Otariidae	Absent	Small	Yes	W shape	Overlapping
Desmotophocidae	Absent	Large	Yes	V shape	Interlocking
Phocidae	Absent	Large	Yes	V shape	Interlocking
Odobenidae	Absent	Large	Yes	Straight	Overlapping

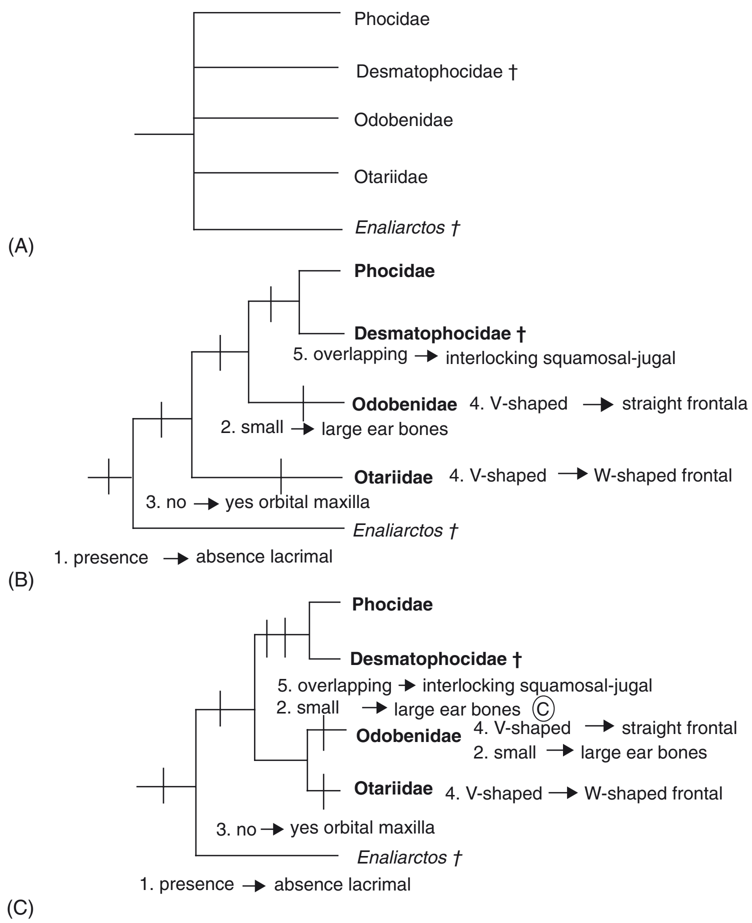

Figure 3 *Three possible cladograms (A–C) of relationships and character-state distributions for the ingroups listed in Table I. Convergence is denoted by circled C. "C" is the currently best accepted hypothesis (Note: morphologic characters used here do not support this arrangement although it is supported by molecular data and total evidence analysis).*

that parsimony is only one of several methods for reconstructing phylogenetic relationship. Other methods such as maximum likelihood and Bayesian approaches are most often used with molecular or combined data, and perform especially well with large data sets (Felsenstein, 2004).

The methods used to search for the most parsimonious tree depend on the size and complexity of the data matrix. These methods are available in several computer programs, e.g., PAUP (Swofford, 2000) and MacClade (Maddison and Maddison, 2000). The latter is particularly useful in assessing the evolution of characters. Systematists are concerned about the relative accuracy of phylogenetic trees (i.e., how much confidence can be placed in a particular phylogenetic reconstruction). Various measures (e.g., tree length) and indices (e.g., consistency index, rescaled consistency index) have been devised to address this concern (Swofford, 2000). Another approach that is often used to estimate the value of a particular cladogram with respect to the data places confidence limits on the individual branches, techniques known as bootstrapping and Bremer support. Another concern stems from the realization that increase in size of the data sets results in a greater chance of the analysis resulting in more than one equally parsimonious trees. A method of working with multiple trees involves the implementation of consensus trees that are useful in identifying the areas of agreement and conflict among competing trees. A related issue in systematics is how to evaluate different data sets (e.g., morphology, behavior, and DNA sequences) particularly how they should be combined (also referred to as "total evidence" or supermatrix approach) (de Queiroz and Gatesy, 2006). The results of "total evidence" or simultaneous analysis of all character data can then be compared with the results of the separate analyses. Before data sets can be combined, it is necessary to determine if they are congruent, that is the order of branching is not contradictory. Several statistical tests have been developed to test for significant incongruencies among data sets. In summary, many factors should be considered in evaluating phylogenetic hypotheses, among the most important is taxonomic sampling, rigorous analysis including the underlying assumptions of various methods, and computer capabilities.

TABLE 2
Classification of Major Lineages of Pinnipeds

Pinnipedimorpha (including *Enaliarctos* and all other pinnipeds)
- Pinnipedia (fur seals, sea lions, seals, walruses, and their extinct relatives
  - Otaroidea (walruses, fur seals, sea lions and their extinct relatives)
    - Otariidae (fur seals and sea lions)
  - Phocomorpha (walruses, seals, and their extinct relatives)
    - Phocoidea (including *Allodesmus*, *Desmatophoca*, seals and walruses)
      - Phocidae (seals)
      - Odobenidae (walruses)

III. Phylogenetic Classification

Taxonomy is the language of biology. One aspect of taxonomy is the classification of organisms which allows us to organize and communicate information about life's diversity. Phylogenetic systematists contend that classification should be based on phylogeny and should include only monophyletic groups. In contrast to monophyletic groups, a paraphyletic group (designated by quotation marks) is one that includes a common ancestor and some but not all of the descendants of that ancestor. An example of a paraphyletic taxon is the "Otarioidea," traditionally recognized as group that includes walruses, otariid seals, and their extinct relatives to the exclusion of

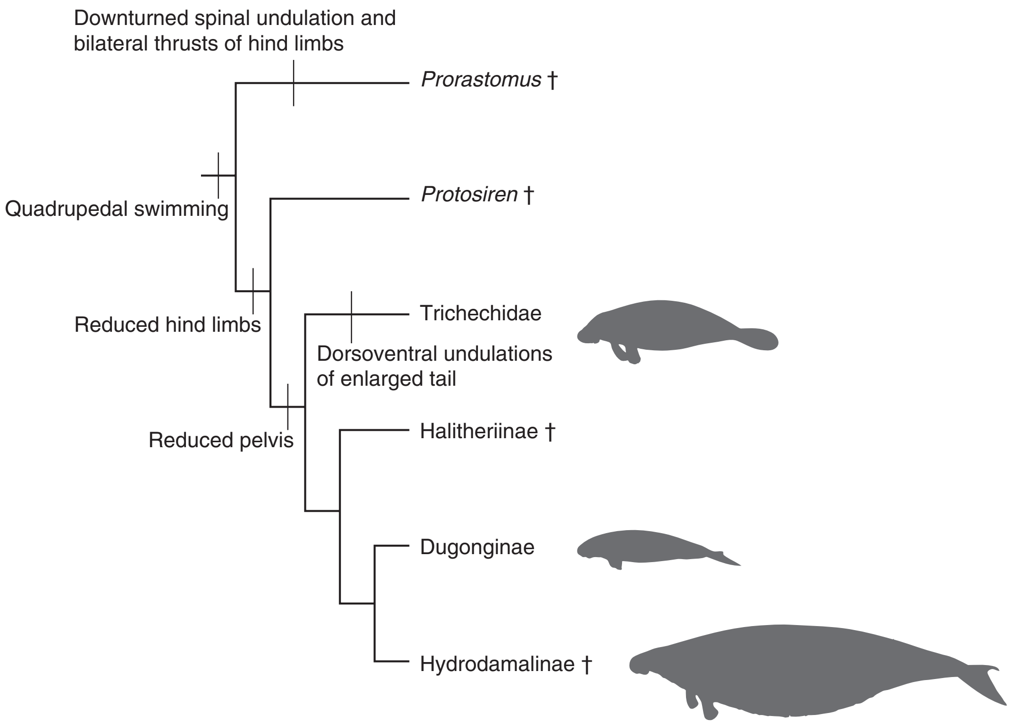

Figure 4 *Evolution of locomotion among sirenians † = extinct taxa. Based on Domning (2000).*

phocid seals (Fig. 1). The recognition of paraphyletic taxa is to be avoided since by doing so we risk misinterpreting the evolutionary relationships of taxa and their classification. One result of the use of phylogenetic methodology is that traditionally accepted ranks (e.g., phylum, class, order, family, genus, and species) often do not correspond to new information about evolutionary relationships among taxa thus rendering their classification misleading. One method is the elimination of rank altogether and the indication of relative rank by subordination as shown by indentation. An example, the classification of major lineages of pinnipedimorphs, is shown in Table II.

IV. Uses of a Phylogeny

Once a phylogenetic framework is produced, one of its most interesting uses is to elucidate questions which integrate evolution, behavior, and ecology. One technique used to facilitate such evolutionary studies is optimization or mapping. Once a cladogram is constructed, a feature or condition is selected to be examined in light of the phylogeny of the group. Among several computer programs recently available for reconstruction of ancestral states and character mapping is Mesquite (Maddison and Maddison, 2006). Examples using marine mammals are becoming more numerous. One of these studies, the evolution of locomotion among sirenians, is briefly reviewed here. A cladogram of relationships among sirenians was first established based on morphologic data. Next, using this phylogenetic framework Domning (2000) (Fig. 4) mapped locomotor characters onto the tree. Sirenians passed through three locomotor stages from a terrestrial quadrupedal ancestry. In the first stage exemplified by archaic sirenians, the prorastomids, swimming was accomplished by alternate thrusts of the hind limbs. This was followed by a second stage seen in the extinct taxon *Protosiren* which employed dorsoventral spinal undulation and bilateral thrusts of the hindlimb in swimming. In a final stage, seen in modern sea cows and manatees, sirenians have evolved into completely aquatic animals swimming with the tail only.

See Also the Following Article

Classification

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