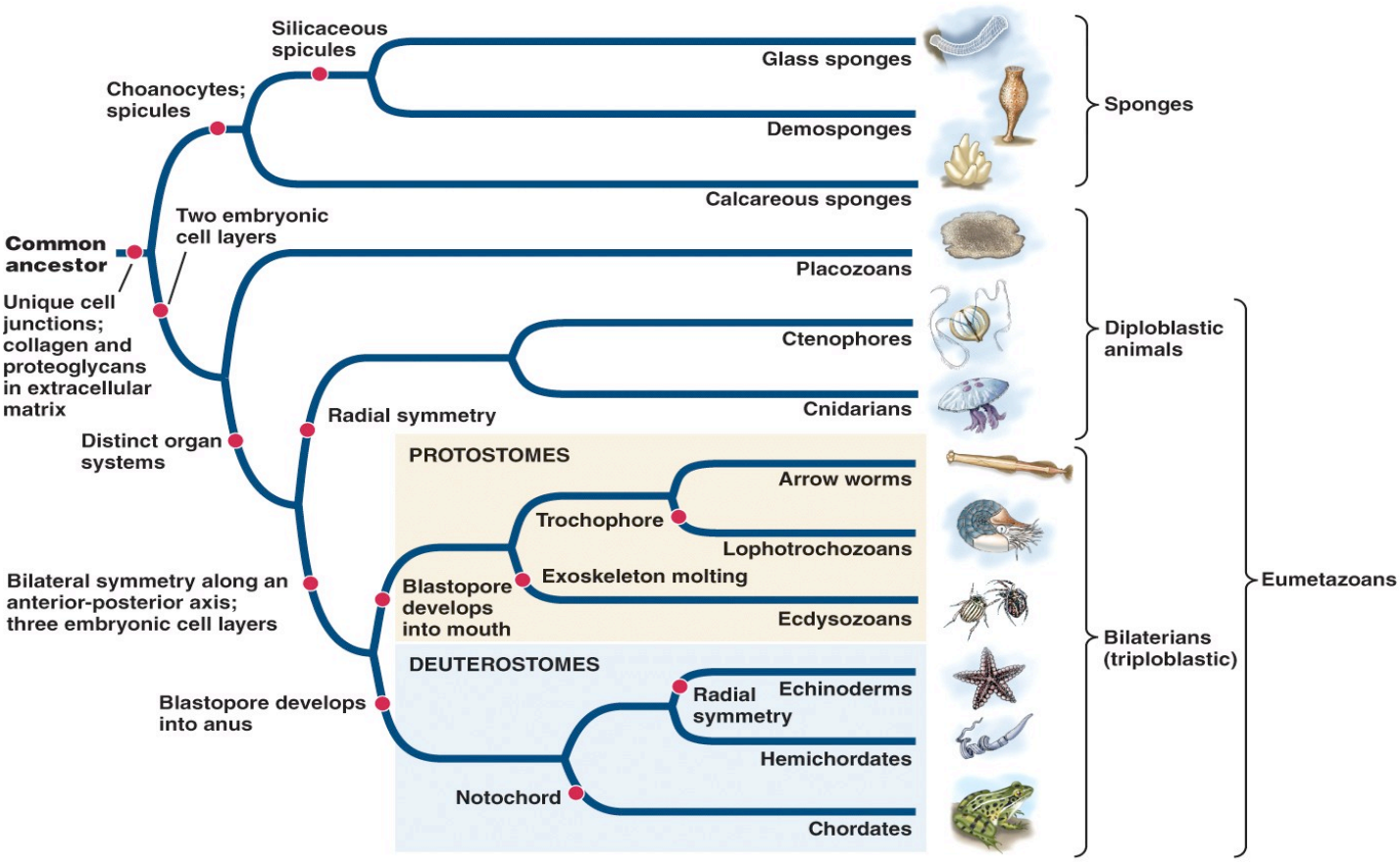
Working With Data from *Principles of Life* by Hillis

Reconstructing Animal Phylogeny



Introduction

The phylogeny of animals has undergone a major revision in recent years. Before it became possible to compare DNA and amino acid sequences from homologous genes and proteins across diverse groups of organisms, biologists mostly used major features of morphology to infer evolutionary relationships across the tree of life. In many cases, these early estimates were supported by subsequent analyses of DNA and protein sequences. However, for organisms that have diverged considerably since they last shared a common ancestor, there are relatively few morphological traits that can be easily compared. Many of the traits that can be compared are general features of the body plan that have evolved repeatedly. For example, Section 23.1 and Figure 23.3 of the textbook describe three types of organization of animal bodies: acoelomates, pseudocoelomates, and coelomates. Biologists once thought that animals with a coelomic cavity were probably all related to one another, and that they were probably derived from pseudocoelomate ancestors, which in turn were derived from acoelomate ancestors. However, recent analyses of the genes shared across all animals have shown that this simple transition is not an accurate reflection of how these groups evolved. Instead, many acoelomates (such as flatworms), and pseudocoelomates (such as rotifers, nematodes, and horsehair worms), have evolved repeatedly from coelomate ancestors, by losing either the mesodermal lining or the entire coelomic cavity. This is usually accompanied by loss of the circulatory system and reduction in size, sometimes as a result of the evolution of a parasitic life cycle.

Several breakthroughs have occurred over the past decade or so as the sequences of many genes and

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proteins have been compared across animals. The first of the major changes in animal phylogeny were supported by sequences of the ribosomal RNA genes, which encode the main structural elements of ribosomes. These sequences are strongly conserved throughout the tree of life, but they show enough evolutionary change to be useful for understanding deep evolutionary relationships. The first major change came with the discovery of one of the two major groups of protostome animals, namely the Lophotrochozoa (Halanych et al., 1995). Once this grouping of highly diverse organisms became clear, it was soon evident that most of the remaining protostomes fell into a group of protostomes that molt (Aguinaldo et al., 1997). This latter group was named the Ecdysozoa. These two large groupings of protostomes were initially quite controversial, but the findings from these early studies of rRNA genes were soon supported by many other sources of data, including many genomic studies (see Dunn et al., 2008; Halanych, 2004; Philippe and Telford, 2006).

As a result of widespread genomic analyses, the relationships among the major groups of animals are becoming clear. In this activity, you will examine a small subset of protein sequences that have been used to understand animal phylogeny.

Original Papers

Aguinaldo, A. M. A., J. M. Turbeville, L. S. Linford, M. C. Rivera, J. R. Garey, R. A. Raff, and J. A. Lake. 1997. Evidence for a clade of nematodes, arthropods and other moulting animals. *Nature* 387: 489–493.
http://www.nature.com/nature/journal/v387/n6628/abs/387489a0.html

Dunn, C. W., A. Hejnol, D. Q. Matus, K. Pang, W. E. Browne, S. A. Smith, E. Seaver, G. W. Rouse, M. Obst, G. D. Edgecombe, M. V. Sørensen, S. H. D. Haddock, A. Schmidt-Rhaesa, A. Okusu, R. M. Kristensen, W. C. Wheeler, M. Q. Martindale, and G. Giribet. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. *Nature* 452: 745–749.
http://www.nature.com/nature/journal/v452/n7188/abs/nature06614.html

Halanych, K. M. 2004. The new view of animal phylogeny. *Annual Review of Ecology, Evolution, and Systematics* 35: 229–256.
http://arjournals.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.35.112202.130124

Halanych, K. M., J. D. Bacheller, A. M. A. Aquinaldo, S. M. Liva, D. M. Hillis and J. A. Lake. 1995. Evidence from 18*S* ribosomal DNA that the lophophorates are protostome animals. *Science* 267: 1641–1643.
http://www.sciencemag.org/content/267/5204/1641.abstract

Philippe, H. and M. J. Telford. 2006. Large-scale sequencing and the new animal phylogeny. *Trends in Ecology and Evoution* 21(11): 614–620.
http://www.cell.com/trends/ecology-evolution/abstract/S0169-5347%2806%2900265-5

Links

The concatenated sequence matrix for the Dunn et al. (2008) study is deposited at TreeBase
http://www.treebase.org

The Tree of Life web project, page on animal phylogeny
http://www.tolweb.org/animals

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Primer on animal phylogeny in Current Biology
http://www.current-biology.com/content/article/fulltext?uid=PIIS0960982206023864

University of California Museum of Paleontology page about animal (Metazoan) phylogeny
http://www.ucmp.berkeley.edu/phyla/metazoasy.html

Analyze the Data

The protein sequences that are used to reconstruct the evolutionary relationships of groups as diverse as animals are much longer than can be presented here. However, the table below is a sample of amino residues from several different proteins that can be used to reconstruct the relationships of these representative species (extracted from Dunn et al., 2008). For comparison, the full dataset used by Dunn et al. (2008) includes data on 11,234 amino acid positions across 77 species of animals. Twenty-seven of these amino acid positions for ten of those species are shown in the table.

Species	Character																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Clam	Y	S	T	G	L	H	E	N	Y	A	R	A	M	R	I	A	L	T	I	V	K	L	S	I	V	I	L
Earthworm	Y	A	T	G	L	H	E	N	Y	P	H	A	M	R	I	A	L	T	I	V	K	L	S	I	V	M	L
Tardigrade	Y	A	T	G	L	H	E	H	Y	K	R	A	M	R	V	A	T	S	I	V	R	L	N	L	V	L	L
Fruit Fly	F	A	T	G	L	H	E	N	Y	K	R	A	M	R	I	A	L	S	I	V	S	L	D	L	V	L	L
Sea Urchin	Y	A	T	G	L	L	E	N	Y	P	N	A	M	R	I	A	L	T	V	I	R	Q	N	L	T	V	K
Human	W	A	A	G	L	R	E	H	Y	P	K	A	I	R	I	S	V	T	V	I	R	Q	N	L	T	V	K
Chicken	W	A	A	G	L	R	E	H	Y	P	R	A	I	R	I	A	V	T	V	I	R	Q	N	L	T	V	K
Lancelet	Y	A	T	G	L	R	E	H	Y	P	K	A	M	R	I	A	V	T	V	I	R	L	N	L	T	V	K
Sponge	Y	G	L	S	L	R	P	N	F	P	K	S	M	S	V	A	L	T	V	I	R	Q	N	L	V	I	L
Outgroup	Y	G	L	G	Q	D	P	N	F	P	K	S	F	S	V	A	L	T	V	I	R	Q	N	L	V	I	L

Question 1

Construct a phylogenetic tree of these ten species using the parsimony method (see Section 16.2 for instructions, and the examples in Table 16.1 and Figure 16.3 of the textbook). Use the outgroup (data from a choanoflagellate) to root your tree. Assume that all changes among amino acids are equally likely.

Question 2

How many changes (from one amino acid residue to another) occur along each branch on your tree?

Question 3

Which amino acid positions (i.e., which character numbers) exhibit homoplasy (convergence or reversal of the character state)?

Question 4

Which group on your tree represents the bilateral animals? The protostomes? The lophotrochozoans? The ecdysozoans? The deuterostomes? The chordates? The vertebrates?