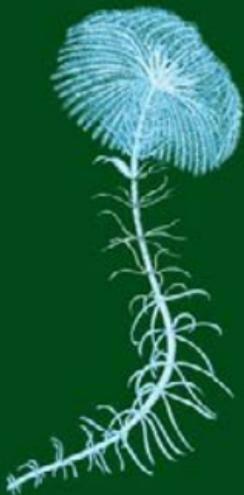


CLAUS NIELSEN

ANIMAL EVOLUTION

INTERRELATIONSHIPS OF
THE LIVING PHYLA

THIRD EDITION



OXFORD

Animal Evolution

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Interrelationships of the Living Phyla

CLAUS NIELSEN

*Natural History Museum of Denmark,
University of Copenhagen*

THIRD EDITION

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PREFACE TO THIRD EDITION

Studies of molecular phylogeny have dominated the biological literature during the last decade, but important new information from morphology and embryology has been obtained, especially with the use of new immunostaining methods. For a period, the molecular results of higher animal phylogeny looked rather chaotic, with many conflicting trees based on studies of mitochondrial and ribosomal genes. However, the trees obtained through the new studies of large numbers of various sequences, of expressed sequence tags, and even on whole genomes, now seem to converge, and a congruence with morphology-based trees seems possible. This has inspired me to make this new edition.

Revisions of larger texts are always in danger of growing, because new material is added and old material not discarded. I have tried to avoid this, for example by using the excellent series *Microscopic Anatomy of Invertebrates*, edited by Frederick W. Harrison (Wiley-Liss, New York, 1991–1999) as a general reference for the anatomy of the various groups; references that can be found in these volumes have generally been excluded. My two papers on the development of trochophora larvae (Nielsen, C. 2004, 2005. *J. Exp. Zool. (Mol. Dev. Evol.)* **302B**: 35–68 and **304B**: 401–447) have been used in the same way.

Many colleagues have helped in various ways; some have sent me illustrations for use in the book and others have read one or more chapters and given good suggestions: S. Amano (Kanazawa University), M. Blaxter (University of Edinburgh), M.J. Dayel

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Mrs Birgitte Rubæk is thanked for fine help with the new illustrations.

Copenhagen
March 2011

PREFACE TO SECOND EDITION

During the years since the text for the first edition of this book was concluded (in 1992), a wealth of new morphological information has become available, including both histological/ultrastructural and embryological data, and new areas, such as numerical cladistic analyses, DNA sequencing, and developmental biology, have become prominent in phylogenetic studies. I have tried to update the information about morphology, but the other fields have been more difficult to deal with; numerical cladistic analyses and molecular phylogeny are discussed in separate chapters, but following my conclusions in these two chapters, I have in general refrained from discussing results obtained through these methods.

I am fully aware that my coverage of molecular studies, including the extremely promising evolutionary developmental biology, is very incomplete. I have tried to select information from studies that appear to describe consistent phylogenetic signals, but my choice is biased by my background as a morphologist. The interested reader is strongly advised to consult a recent textbook or review articles on the subject.

Once again it is my pleasure to thank the many generous colleagues who have helped me in various ways, especially those who have read drafts of various chapters and given many good comments: André Adoutte (Paris), Wim J.A.G. Dictus (Utrecht), Andriaan Dorresteijn (Mainz), Danny-Eibye-Jacobsen (Copenhagen), Peter W.H. Holland (Reading), Reinhardt Møbjerg Kristensen (Copenhagen), Thurston C. Lacalli (Saskatoon), George O. Mackie (Victoria), Mark Q. Martindale (Hawaii), Rudolf Meier (Copenhagen), Edward E. Ruppert (Clemson), George L. Shinn (Kirksville), Nikolaj Scharff (Copenhagen), Gerhard Scholtz (Berlin), Ralf Sommer (Tübingen), Martin Winther Sørensen (Copenhagen), Gregory A. Wray (Durham), Russel L. Zimmer (Los Angeles). None of them should be held responsible for the ideas expressed here.

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PREFACE TO FIRST EDITION

No naturalist can avoid being fascinated by the diversity of the animal kingdom, and by the sometimes quite bizarre specializations that have made it possible for the innumerable species to inhabit almost all conceivable ecological niches.

However, comparative anatomy, embryology, and especially molecular biology, demonstrate a striking unity among organisms, and show that the sometimes quite bewildering diversity is the result of variations over a series of basic themes, some of which are even common to all living beings.

To me, this unity of the animal kingdom is just as fascinating as the diversity, and in this book I will try to demonstrate the unity by tracing the evolution of all of the 31 living phyla from their unicellular ancestor.

All modern books on systematic zoology emphasize phylogeny, but space limitations usually preclude thorough discussions of the characteristics used to construct the various phylogenetic trees. I will try to document and discuss all the characters that have been considered in constructing the phylogeny—both those that corroborate my ideas and those that appear to detract from their probability.

In the study of many phyla, I have come across several important areas in which the available information is incomplete or uncertain, and yet other areas that have not been studied at all; on the basis of this I have, for each phylum, given a list of some interesting subjects for future research, and I hope that these lists will serve as incentives to further investigations.

It should be stressed that this book is not meant as an alternative to the several recent textbooks of systematic zoology, but as a supplement, one that I hope will inspire not only discussions between colleagues but also seminars on phylogeny—of the whole animal kingdom or of selected groups—as an integrated part of the teaching of systematic zoology.

The ideas put forward in this book have developed over a number of years, and during that period I have benefitted greatly from interactions with many colleagues. Some have been good listeners when I have felt the need to talk about my latest discovery; some have discussed new or alternative ideas, names or concepts with me; some have provided eagerly sought pieces of literature or given me access to their unpublished results; and some have sent me photos for publication. To all these friends I extend my warmest thanks; no names are mentioned, because such a list will inevitably be incomplete. A number of colleagues have read one to several chapters (the late Robert D. Barnes (Gettysburg) and Andrew Campbell (London) have read them all) and given very valuable and constructive comments that I have often but not always followed; I want to mention them all, not to make them in any way responsible, but to thank them for the help and support that is necessary during an undertaking such as this: Quentin Bone (Plymouth), Kristian Fauchald (Washington, DC), Gary Freemann (Austin), Jens T. Høeg (Copenhagen), Åse Jespersen (Copenhagen), Niels Peder Kristensen (Copenhagen), Margit Jensen (Copenhagen), Reinhardt Møbjerg Kristensen (Copenhagen), Barry S.C. Leadbeater (Birmingham), Jørgen Lützen (Copenhagen), George O. Mackie (Victoria), Mary E. Petersen (Copenhagen), Mary E. Rice (Fort Pierce), Edward E. Ruppert (Clemson), Amelie H. Scheltema (Woods Hole), George L. Shinn (Kirksville), Volker Storch (Heidelberg), Ole S. Tendal (Copenhagen), and Russell L. Zimmer (Los Angeles).

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