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# Origin and Evolutionary Radiation of the Mollusca

Edited by

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# CONTENTS

List of contributors	xi
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## Part I Origin of Mollusca and evolution of the major groups

1. The Mollusca: coelomate turbellarians or mesenchymate annelids? GERHARD HASZPRUNAR	3
2. Synapomorphies and plesiomorphies in higher classification of Mollusca LUITFRIED v. SALVINI-PLAWEN & GERHARD STEINER	29
3. Phylogenetic position of Sipuncula, Mollusca and the progenetic Aplacophora AMÉLIE H. SCHELTEMA	53
4. Origin of Aculifera and problems of monophyly of higher taxa in molluscs DMITRY L. IVANOV	59
5. An evolutionary tree for the Mollusca: branches or roots? DAVID R. LINDBERG & WINSTON F. PONDER	67
6. Early evolution of the Mollusca: the fossil record BRUCE RUNNEGAR	77
7. Ultrastructure of the heart-kidney complex in smaller classes supports symplesiomorphy of molluscan coelomic characters M. PATRICIA MORSE & PATRICK D. REYNOLDS	89
8. Molluscan sperm ultrastructure: correlation with taxonomic units within the Gastropoda, Cephalopoda and Bivalvia JOHN M. HEALY	99
9. Shell pores (caeca, aesthetes) of Mollusca: a case of polyphyly SONJA REINDL & GERHARD HASZPRUNAR	115
10. Evolution of high-latitude molluscan faunas J. ALISTAIR CRAME	119

## Part II Gastropod evolution

11. Gastropod phylogeny — challenges for the 90s WINSTON F. PONDER & DAVID R. LINDBERG	135
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12. The significance of the early cleavage pattern for the reconstruction of gastropod phylogeny 155  
JO A.M. van den BIGGELAAR
13. Patterns of morphologic diversification during the initial radiation of the "Archaeogastropoda" 161  
PETER J. WAGNER
14. Anatomy and affinities of lepetid limpets (Patellogastropoda = Docoglossa) 171  
GEORG ANGERER & GERHARD HASZPRUNAR
15. Phylogeny and patterns of evolutionary radiation in trochoidean gastropods 177  
CAROLE S. HICKMAN
16. Evolutionary systematics of Jurassic Trochoidea: the family Colloniidae and the subfamily Proconulinae 199  
STEFANO MONARI, MARIA ALESSANDRA CONTI and JANOS SZABÓ
17. The *Littorina saxatilis* species complex — interpretation using random amplified polymorphic DNAs 205  
SUSAN CROSSLAND, DAVID COATES, JOHN GRAHAME & PETER J. MILL
18. Evolutionary radiations in the Cypraeidae 211  
E. ALISON KAY
19. Phylogeny and relationships of Neogastropoda 221  
YURI I. KANTOR
20. The Diaphanidae as a possible sister group of the Sacoglossa (Gastropoda, Opisthobranchia) 231  
KATHE R. JENSEN
21. Development and homologies of the anal gland in *Haminaea navicula* (Da Costa, 1778) (Opisthobranchia, Bullomorpha) 249  
KURT SCHAEFER
22. Contrasting developmental strategies and speciation in N.E. Atlantic prosobranchs: a preliminary analysis 261  
MARCO OLIVERIO
23. Phylogenetic relationships of the pulmonate gastropods from rRNA sequences, and tempo and age of the stylommatophoran radiation 267  
SIMON TILLIER, MONIQUE MASSELOT and ANNIE TILLIER
24. Relationships within the Ellobiidae 285  
ANTÓNIO M. de FRIAS MARTINS

55	25. Parallelism in the origin of the G-type clausilial apparatus (Gastropoda, Pulmonata, Clausiliidae) EDMUND GITTENBERGER & MENNO SCHILTHUIZEN	295
51	26. Allozyme variation in some Cretan <i>Albinaria</i> (Gastropoda): paraphyletic species as natural phenomena MENNO SCHILTHUIZEN & EDMUND GITTENBERGER	301
71	27. Crab predation as a selective agent on shelled gastropods: a case study of <i>Calliostoma zizyphinum</i> (Prosobranchia: Trochidae) S. JANE PRESTON, DAVID ROBERTS, & W. IAN MONTGOMERY	313
77	<b>Part III Evolution of scaphopods and bivalves</b>	
99	28. Suprageneric phylogeny in Scaphopoda GERHARD STEINER	329
105	29. The evolutionary history of the Bivalvia BRIAN MORTON	337
111	30. The early evolution of the Bivalvia JOHN C.W. COPE	361
117	31. The phylogenetic significance of some anatomical features of bivalve veliger larvae SIMON M. CRAGG	371
121	Index	381

sperm/spermiogenic features seem to isolate the Crassatelloidea + Carditoidea from other heterodonts, including the Leptonoidea. These features include the elongate and narrow shape of the acrosome and nucleus (both usually shorter and wider in other heterodonts with the notable exception of the tellinoidea *Scrobicularia plana*: Sousa *et al.*, 1989), presence of a centriolar rod instead of a proximal centriole (proximal centriole present in all other heterodonts), 8-9 tightly pressed mitochondria (4-5 in other heterodonts), spermatid nuclear condensation involving formation of fibres and lamellae (condensation by granules, or rarely fibres in other heterodonts). Until more comparative information on bivalve sperm becomes available, it seems best to retain the Crassatelloidea + Carditoidea within the Heterodonta.

#### *Subclass Anomalodesmata (Fig. 8.3D)*

To date three families of this subclass, all members of the Pandoroidea, have been investigated for sperm ultrastructure: Lyonsiidae (Kubo *et al.*, 1979); Laternulidae (Kubo, 1977); Myochamidae (Popham, 1979; Healy this paper). In addition, sperm of one species of Thracioidea (Thraciidae) has been briefly examined using light microscopy (Franzén, 1955). The Claedoheridae, Pandoridae, Periplomatidae and the superfamilies Pholadomyoidea, Clavagelloidea and Poromyoidea remain unstudied. Anomalodesmatan sperm are characterized by three unusual features: (1) a posteriorly positioned acrosome (the 'temporary acrosome' of Kubo, 1977; acrosome claimed to be absent in *Thracia* by Franzén, 1955); (2) a slightly to markedly elongate distal centriole and (3) an asymmetrical arrangement of mitochondria at the base of the nucleus (see Fig. 8.3D). Developmentally, the 'temporary acrosome' is a true, Golgi-derived acrosomal vesicle, which is positioned at the nuclear apex during mid-spermiogenesis, but subsequently moves posteriorly and positions itself close to the mitochondria, at the base of the nucleus (Kubo, 1977; Healy this paper). As far as is known, this phenomenon is unique to the Anomalodesmata, and therefore a likely autapomorphy. In this regard it would be interesting to examine sperm ultrastructure in the unstudied anomalodesmatan families (eg Claedoheridae, Clavagellidae) to check for presence of a 'temporary acrosome'. Of particular importance would be observations on the sperm of the primitive but exceptionally rare anomalodesmatan *Pholadomya candida* (sole living species of Pholadomyidae, Pholadomyoidea).

Inclusion of the Cuspidariidae within the Anomalodesmata by some authors (eg Newell, 1969; Allen, 1985; Morton, 1985) is not supported by sperm ultrastructure. Sperm of *Cuspidaria* sp. (Figure 8.3 this paper) possess an anteriorly positioned acrosomal vesicle which resembles more closely the acrosomes of certain heterodonts such as the myoidean *Notocorbula vicaria* (Popham, 1979) rather than those of the Pandoroidea. After a consideration of patterns of gill

innervation, Salvini-Plawen and Haszprunar (1982) concluded that the Septibranchia contained two unrelated groups — the Verticordiidae and the Cuspidariidae + Poromyidae. They were unsure as to whether the Cuspidaria + Poromyidae ('Poromyida') were of heterodont or anomalodesmatan affinities, but did suggest a possible connection with Myidae, which is at least consistent with available sperm data. Disassociation of the Cuspidariidae from the Anomalodesmata is not a new concept, as discussed by Runnegar (1974). In this context, a study of sperm morphology in the remaining two septibranch families (Verticordiidae and Poromyidae) may help in determining whether these groups should be retained in or excluded from the Anomalodesmata.

#### *Subclass Palaeoheterodonta (Fig. 8.3E)*

It has long been believed that the largely extinct marine Trigonioidea were closely related to the Unionoidea (freshwater mussels) (see Cox, 1960 and Morton, 1987 for background discussion to this topic). This view was based on certain conchological similarities (tooth structure, shell microstructure and scars, shell sculpture facies) and certain anatomical similarities (ctenidial ciliation). Although some of these similarities have been shown to be erroneous or tenuous (Morton, 1987), ultrastructural studies have demonstrated that the Unionoidea and Trigonioidea also share a highly unusual and, at least within the Mollusca, unique sperm feature, namely the presence of multiple acrosomal vesicles (unionoid *Velusunio ambiguus*, and three species of *Neotrigonia*, Healy, 1989c and this paper; see Fig. 8.3). This similarity cannot be interpreted as a convergent response to environmental factors because unionoids fertilize within the mantle cavity, while trigonioids fertilize externally (Tevesz, 1975). I therefore consider that similarities between sperm of *Neotrigonia* and unionoids reflect a true phylogenetic relationship between the Trigonioidea and Unionoidea. Although two recent studies have claimed that unionoid sperm possess only a single acrosomal vesicle (Rocha and Azevedo, 1990) or none at all (Peredo *et al.*, 1990), my own studies of *Velusunio ambiguus* (Healy, 1989) have clearly shown the presence of a multivesicular acrosomal complex. Possibly in certain unionoids a late fusion of proacrosomal vesicles may occur (Rocha and Azevedo, 1990). A detailed investigation of more unionoid genera and particularly members of the most primitive unionoid family, Margaritiferidae, may show whether or not unionoid proacrosomal vesicles can indeed fuse.

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